REGENERATION OF *JUNIPERUS PROCERA* AND *AFROCARPUS GRACILIOR* IN THE AFROMONTANE FORESTS OF ETHIOPIA

by

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DECLARATION

This thesis and the work presented herein is my own work except where otherwise indicated, and no part of it has been presented for a higher degree.

H. Sharew, September 1994

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MEMORIAL

In loving memory of my father, Captain Sharew Dessalegne

DEDICATION

This thesis work is respectfully dedicated to all those who, through thoughts, word or deed, demonstrated their belief to the careful planning and wise use of forests and related resources to improve urban and rural environments so as to reinstate the natural balance and provide a sustainable ecosystem to the present and future generation.

ABSTRACT

The work seeks to elucidate the conditions for growth of seedlings in an Afromontane forest. The species studied were *Juniperus procera* Hochst. ex Endl. and *Afrocarpus gracilior* (Pilger) C.N. Page from the dry montane coniferous forests of Ethiopia. The main aim was to provide the necessary information for a silviculture based on natural regeneration.

The understorey light climate was examined, particularly the photosynthetic photon flux (PPF) and Red:Far-red ratio. An empirical model was developed linking measured PPF to gap fraction as assessed from hemispherical photographs. Air temperatures and soil moisture contents were measured, and comparisons made with an 'open' site. The effects of burning and mechanical scarification on regeneration following clear felling and timber extraction were assessed. Finally, a programme of controlled environment experiments was carried in Edinburgh. The effects of seed pre-germination treatments and simulated forest canopy light on seed germination were tested; the responses of seedlings to simulated forest canopy light conditions and nutrient supply were measured, and the response of seedlings to Red:Far-red ratio was examined.

The main findings were: (i) The forest is relatively 'open' with a mean photon flux density at the forest floor of 1.4 mol m^{-2} d^{-1} to 12.7 mol m^{-2} d^{-1}, and little annual variation. There is a mean Red:Far-red ratio in the range of 0.54 to 0.67 in the forest understorey. (ii) Clear cutting or manipulating the canopy alone did not result in the regeneration of both species, but regeneration and establishment of *Juniperus procera* could be enhanced by site preparation, particularly controlled burning, which exposes the mineral soil. (iii) In the laboratory, none of the pre-germination treatment improved the percentage germination of *J. procera*, but cutting the seed coat at the radical end improved the percentage germination of *A. gracilior*. (iv) *J. procera* seeds were unresponsive to the presence or absence of light for germination, whilst complete darkness enhanced germination of *A. gracilior*. (v) Both species are able to survive at photon flux densities as low as 2 mol m^{-2} d^{-1} or 46 µmol s^{-1} m^{-2}, but *A. gracilior* demonstrated more shade tolerance than *J. procera*. (vi) In both species an enhanced nutrient supply, shifted the allocation of biomass between plant parts. (vii) Both species responded to low R:F-r ratio by an increased stem extension.

The results are discussed in relation to the silvicultural needs of Ethiopia. Ground vegetation should be disturbed. Site treatments that reduce logging waste and expose mineral soils are recommended. In particular controlled burning following 'clearcutting in strips' where seed is available from adjacent stands is likely to be the most practical silvicultural tool to achieve maximum regeneration of *J. procera*.

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CHAPTER 1

General Introduction and Literature Review

1.1 Introduction and background

Natural forests have been exploited and cleared, aand have suffered man-made damage resulting in a gradual decline in extent. Only in the last 150-200 years has net destruction of forest taken place in almost every country and, in recent years, this rate of disappearance has increased sharply in tropical countries (Evans, 1992). This deforestation is widely believed to be having direct and immediate effect on the environment, increasing soil erosion, flooding and droughts; it may have unforeseen long-term consequences, like changes in the weather and loss of productivity, that may hinder Man's ability to sustain life in tropical regions (Brown and Wolf, 1985).

Land clearing in tropical forests involves the modification of complex ecosystems by partial or complete removal of existing vegetation so that the land may be used for purposes other than management of natural forests. Generally speaking, the issues surrounding tropical land clearance are more complex than corresponding issues in temperate regions. High rates of precipitation with relatively higher temperatures, which accelerate degradation of soils, are instrumental in removing soil and soil nutrients by leaching and erosion, and create potentially unstable environmental conditions.

The commercial loggers tend to harvest selectively, only removing a small proportion of wood of a few selected species available, but damaging and impoverishing large areas in their operations. These operations can destroy up to 2/3 of the remaining trees, and roads, haulage tracks and dumping zones can account for 10-30% of the forest area (Burgess, 1973).

Unmanaged over-expliotation of the most sought-after species in the Afromontane zone - notably *Juniperus procera* Hochst. ex Endl. during the past few decades has caused a sharp decline in the extent of the species throughout its range (Hall, 1984; FAO, 1986; Jone, 1989; Negussie *et al.*, 1991). The situation is very similar for *Afrocarpus gracilior* (Pilger) C. N. Page, for instance in Ethiopia, where it is reduced to a

few inaccessible areas (Chaffey, 1979). Continuous and increased over-grazing and destruction by fire, particularly of *J. procera*, have also contributed to the gradual decline of the tree to the verge of extinction (Gardner, 1926; Hall, 1984). The scarcity of viable seed of *J. procera* is also believed to have contributed to its decline. The well known unreliability of *J. procera* seed germination (e.g. Negussie *et al.*, 1991) in its natural range has been a constraint limiting the success of attempts to develop it as a major, widespread commercial species. To further worsen the situation *J. procera* does not regenerate under natural conditions of closed canopy owing to the extreme shading, and its seeds do not germinate on areas of thick humus surface (Gardner, 1926; Hall, 1984).

Natural forests throughout the world are fundamentally similar in their patterns in space and time because the same processes of succession and maintenance operate (Whitmore, 1982). These patterns and processes of change in a forest are expressed by a growth cycle in which three arbitrary phases are always altering as one phase changes to the next. The coarseness depends on what creates the gaps. These gaps are heterogeneous and vary from a few metres to several kilometres across. Such gaps play a very important role in the processes of natural regeneration on the forest floor.

When gaps are created in the forests by logging they are recolonised as in the natural disturbances in primary forest. This process of re-colonisation involves a great diversity of interactions among and between plants and animals, and results in a new forest with a different set of species. Each species may have quite different ecological requirements. The success of any species depends on its growth rate, which in turn depend on physiological flexibility that facilitates its competition for light and nutrient requirements relative to competitors, and nutrient availability. However, following the disturbance of a forest stand, the filling of the gaps with economically desirable species is not always ensured, and depends on the treatments used to direct succession toward forestry goals. The potential rate and course of succession vary widely among forest types and can be significantly altered by silvicultural activities such as site preparation and release operation. However, in order to provide the correct treatment at the right time and achieve the objectives of management, much needs to be known about the environmental variables and characteristics of the vegetation of particular stands, and ecological requirements of the desirable species.

General methods of regeneration practiced in the tropical forests and their relative success have been reviewed by Gómez-Pompa and Burley (1991), while the

regeneration methods in the temperate zone are reviewed by Matthews (1989). Regeneration in the tropical forests following disturbance, by logging or clearcutting may occur as a result of coincidence of favourable conditions (Nair, 1991), and is often difficult to achieve. But the lack of knowledge on the requirements of individual species has been considered as one of the main causes of failure (Nair 1991; review by Gómez-Pompa and Burley, 1991). Effective management of natural forests for timber production in the tropics does not exist except for parts of India and Trinidad (Evans, 1992). In Suriname, successful experimental scale trials have existed (de Graaf, 1986). Sometimes, even when regeneration is present, drastic changes in light and moisture conditions consequent to canopy opening adversely affect the establishment and growth of seedlings (Nair, 1991).

Despite renewed interests in indigenous tree species in tropical east Africa, afforestation success with some valuable multipurpose species is limited mainly because of the lack of appropriate silvicultural knowledge and difficulties which they present during the whole or part of their life cycle. Consequently, one of the greatest problems faced today in east Africa and Ethiopia is the rapidly rising rate of extinction of wild plant species (Schimozono and Iwatsuki, 1986).

Clear cutting a dense conifer stand with little understorey is said by some people to provide excellent conditions for regrowth (Walstad *et al.*, 1987). On the other hand, harvesting methods that minimize disturbance in sparsely stocked stands, and harvesting of conifer or mixed conifer-broadleaved stands are likely to create post harvesting problems with the residual vegetation. Furthermore, harvesting methods that physically disturb the surface soil, although providing some control of sprouting species, can lead to rapid colonization by pioneering grasses, forbs, shrubs and other broadleaved species - all of which can impede or suppress conifer regeneration (Walstad *et al.*, 1987). Thus, in order to achieve successful regeneration some additional treatment of ground vegetation, litter layer and logging waste is generally needed following harvesting operations.

Ecological studies in tropical forests have focused almost entirely on the tropical rainforest or moist forests. It is becoming increasingly important to extend these ecosystem and regeneration studies into the coniferous forests, which mainly occupy mountain regions, and which may have an important additional role in watershed management. The lack of ecological research into the dynamics of the coniferous forests makes it virtually impossible to make positive recommendations to foresters as

to their environmental and silvicultural requirements for the method of regeneration to be practiced.

The present study lays the foundation for a long term scientific management of regeneration in the Afromontane coniferous forests. For the maintenance of ecological diversity and sustained timber yields, proper management of primary or secondary forests is needed. Plantation forestry is also required for the production of timber, but it would be a big mistake to assume that plantations are the only answer for future wood supplies. Continuous research is needed on the ecology of tropical broad-leaved and coniferous forest species so that their management is practicable to the point of being economically worthwhile as one way of saving them for the products they yield and the environment they protect. Whichever form of forestry is employed, a thorough understanding of forest environment, together with a knowledge of ecophysiological differences between the species that constitute the forest, are a prerequisite of a successful silvicultural system. Thus, the next sections of this introduction will serve to briefly review the literature on forest microenvironement, particularly the light environment, plant response to light, nutrient availability, forest harvesting practices and techniques of site preparation with particular reference to forest regeneration.

1.2 Forest microenvironment

The main goal of forest regeneration is to stock a site with desirable tree species following logging or other disturbances. To effectively accomplish this goal, the manner in which trees interact and respond to their environments must be known. Knowledge of the ecological principles that govern plant growth and distribution is essential for forest management, for it is through study and application of ecological concepts that the problems of forest regeneration will be solved.

The forest microenvironment is influenced by physical characteristics (rocks, debris, soil type, plants) and topography (slope and aspect) (e.g. Fowells and Means, 1990). The microenvironment is modified when trees are cut or forests are regenerated. Environmental resources directly consumed by plants include light, water, nutrients and the gases necessary for photosynthesis and respiration. Factors such as temperature, soil compaction, and grazing, are the environmental conditions which influence the survival and growth of plants. Forest clearing or cultivation modifies the

microclimate of a site and thereby influences the appearance of and composition of vegetation. Thus, forest regeneration is based on the physiological and morphological responses of tree seedlings to the available resources and suitability of conditions that occur on a site.

A dense forest canopy drastically modifies climate near the ground. Some of the effects of forest canopy on microclimate given by Lee (1978) are summarized next:

1. Radiation measured near the ground is usually less than that above the canopy by at least an order of magnitude during clear days.

2. Wind speed is reduced to an extent that depends on the openess of the canopy.

3. The relative amount of precipitation that reaches the forest floor varies with both the interception (storage) capacity of the canopy and the intensity and duration of precipitation. On average, rainfall deficits under mature broadleaved canopies may vary from less than 10% during the leafless period to more than 20% during the growing season; the average deficits are usually greater under coniferous types especially during the dormant season.

4. During the periods when the radiation balance is positive; air temperatures near the forest floor are less than those at the top of the canopy; at night when the radiation balance is zero or negative, air near the forest floor is slightly warmer than it is above the canopy.

5. Relative humidity (RH) near the ground exceeds that above the canopy during the day primarily because of the temperature differences; at night with virtually isothermal conditions, higher relative humidities occur near the forest floor because the ambient vapour pressure is greater at that level.

6. Carbon dioxide is also higher near the ground than above the canopy.

Thus, regeneration and growth of seedlings at the forest floor is likely to be influenced by all of these factors. But the over-riding effect of light climate is generally accepted.

1.2.1 Light levels at the forest floor

The amount of light reaching the forest floor depends on the density of foliage through which it passes. Although the methods and equipment used by different workers to measure relative irradiance varied a lot there was a general similarity in the values that were reported for the forest floor of tropical moist and sub-tropical forests (Table 1.1). It is clear from the above review that little photosynthetic photon flux (PPF) reaches the forest floor. Thus, it is important to look into the spectral distribution of the light that reaches the forest floor passing through the vegetation canopy, in order to understand the growth of understorey plants under the influence of very low PPF.

Table 1.1: Estimation of percentage photosynthetic photon flux (PPF) received at the forest floor of different forest vegetation types

Forest	Light %	References
i) Tropical broadleaved forests:		
South Brazil	<1	McLean (1919)
Barro Colorado Island in Panama	≈3	Allee (1926)
Nigeria tropical moist forests	2-5	Evans (1956)
Singapore tropical moist forests	2-5	Whitmore and Wong (1959)
Sub-tropical forests, Southern Queensland, Australia	2	Björkman and Ludlow (1972), in Torquebiau (1988)
Temperate forests		
Coniferous forest, Vancouver Island, British Columbia, Canada	16.5	Vales and Bunnell (1988)
Douglas-fir forest, Cascade Mountains, USA	0.6	Canham *et al.* (1990)
Nothern hardwood forest, Ohio, USA	1.3	Canham *et al.* (1990)
Southern hardwood forest, southeast USA	1.3	Canham *et al.* (1990)
Spruce - balsam fir forest, Great Smoky Mountain, USA	5.2	Canham *et al.* (1990)
Boreal forests		
Birch - spruce forest, boreal	2	Larcher (1980)
Pine forests	2	Larcher (1980)

1.2.2 Vegetation shadelight

This subject has been reviewed by Morgan and Smith (1981). Light reaching the forest understorey habitat has two main components: (1) Unfiltered daylight (direct sunlight, diffuse skylight or diffuse light from the clouds) which has passed through holes in the canopy. (2) Filtered or attenuated daylight, the spectrum of which has been altered by the canopy through the process of absorption, reflection and transmission. The most important aspect of shadelight is that it affects growth and development of understorey plants where both quantity and quality of light has been altered. Climatic conditions have only a small effect on the spectrum of vegetational shadelight whilst vegetation structure and density have large effects (Morgan and Smith, 1981).

The quantitative and qualitative changes in the available energy in the understorey include the following (Holmes, 1981; Chazdon and Fetcher, 1984; Lee, 1987):

1. Light passing through vegetation is attenuated in PPF (400-700 wavelength), and hence the quantity of photosynthetically active radiation is reduced.

2. There is a marked reduction in the quantity of radiation in the blue part of the spectrum.

3. A strong depletion of the red waveband and relatively weak attenuation of the far-red waveband is evident.

Due to these changes in the spectrum, the forest shadelight is characterized by low PPF, a low proportion of blue light, and low red to far-red ratio (R:F-r). The low R:F-r ratio is known to be especially important in plant photomorphogenesis (review by Smith, 1986). Holmes and Smith (1977) provide a detailed analysis of spectral energy distribution under plant canopies.

The light which passes through openings of forest canopy and its contribution to the processes of growth and development of tree seedlings at the forest floor will be considered first.

i) Sunflecks

Sunflecks are a special case of vegetational shadelight caused by the penetration of predominantly direct solar radiation through openings in the forest canopy. Because of their penetration through the canopy, the spectral quality of sunflecks differs from that of diffuse shadelight (Chazdon and Fetcher, 1984b; Lee, 1987). They are composed of direct sunlight, sunlight reflected from vegetation, diffuse skylight and vegetation-filtered diffuse skylight (Morgan and Smith, 1981). The relative proportions of diffuse and direct sunlight in sunflecks may vary greatly, but direct sunlight predominates at the centre of all sunflecks (Holmes and Smith, 1977b). This relative proportion can be partly explained by penumbral effects within forest canopies (Anderson and Miller, 1974) or partial shadow at the edge of the sunfleck. The relative importance of the penumbra in the forest understorey depends on the size of canopy opening and the height of canopy (Oker-Blom, 1984). A canopy opening of a diameter at least equal to the apparent size of the solar disk (a solid angle of ½°) is required to transmit full-sun irradiance.

Sunfleck sizes will be small, and penumbras will be frequent in tall vegetation with small openings (Anderson and Miller, 1974; Oker-Blom, 1984). Under this condition irradiance during sunflecks will be considerably lower than that of direct radiation above the canopy, and the light level and spectral composition will resemble those of shadelight. With increasing canopy gap the spectral distribution tends towards that of daylight from clear sky. Hence, a rapidly fluctuating light may occur. Consequently PPF might vary by over two orders of magnitude within few minutes, and therefore photosystems require to be capable of harvesting very low flux densities of photons, but at the same time tolerate the photon fluxes of sunflecks without the occurrence of photodestruction.

Thus, timing and intensity distributions of sunflecks are probably important determinants of the adaptations of the photosynthetic apparatus to utilize them efficiently. Sunflecks occurring at short and frequent intervals may be utilized efficiently since the photosynthetic apparatus may effectively integrate the light, resulting in higher photosynthetic rates than those long and prolonged steadystate sunflecks at high and low light levels (Pearcy, 1983). More widely spaced sunflecks or single, short sunflecks occurring in isolation from others may not be utilized as efficiently because of an activation requirement of the photosynthetic apparatus (Gross and Chabot, 1979) or stomatal limitations (Wood and Turner, 1971). Canopy

movement may be of considerable importance, since it causes rapid light changes but probably lengthens total exposure time and may increase total CO_2 uptake, relative to single, more slowly changing sunflecks expected under still conditions (Pearcy, 1983).

The duration, contribution and importance of sunflecks to understorey plants of different forest types has recently been reviewed by Chazdon (1988). Table 1.2 provides the contribution of sunflecks reported by various authors in both temperate and tropical forests.

Table 1.2: The percentage of total radiant energy and total PPF contributed by sunflecks in the understorey of temperate and tropical forests. From Chazdon (1988).

	Forest type/site	Percentage	Reference
i)	**Total radiant energy**		
(a)	TEMPERATE DECIDUOUS FOREST:		
	Tennessee, USA (Summer)	50	Hutchison and Matt (1976, 1977)
(b)	CONIFEROUS FOREST:		
	Connecticut, USA (Summer)	50	Reifsnyder *et al.* (1971)
(c)	LOWLAND TROPICAL EVERGREEN FOREST:		
	Nigeria (1 day)	10	Evans (1939, 1966)
	Nigeria (Jan-Mar)	70	Evans (1956)
	Singapore (entire year)	50	Whitmore and Wong (1959)
	Ecuador (1 day)	60	Grubb and Whitmore (1967)
ii)	**Total PPF**	Percentage	Reference
(a)	TEMPERATE DECIDUOUS FOREST:		
	Michigan, USA (Summer)	45-55	Weber *et al.* (1985)
(b)	LOWLAND TROPICAL EVERGREEN FOREST:		
	Queensland, Australia (1 day)	62	Björkman and Ludlow (1972)
	" (1 day)	12-65	Pearcy (1988a)
	Hawaii, USA (5 weeks)	40	Pearcy (1983)
	Costa Rica (3 days)	10-78	Chazdon (1986)
	Mexico (1 day)	16-44	Chazdon, Field and Pearcy (unpublished)

ii) Spectral distribution

There are large differences in attenuation between the far-red and visible radiation in all vegetational shadelight (Morgan and Smith, 1981), which is a striking aspect of spectral irradiance which varies with depth in a plant canopy (Ross, 1975). A detailed account of the spectral distribution of shade is given by Smith (1981). He showed a substantial drop in the R:F-r ratio under a stand of vegetation. He was also able to demonstrate the possibilities of reducing R:F-r ratios experimentally to those found in natural plant communities using specially constructed light-quality cabinets, and found values ranging from approximately 0.2 to 3.0.

Morgan and Smith (1981a) give a R:F-r ratio value of 1.15 for daylight and review R:F-r ratios reported by different authors under different conditions for various vegetation types (Table 1.3). Chazdon and Fetcher (1984) and Lee (1987) also give a R:F-r ratio value of between 1.10 to 1.25 under full sun and as low as 0.10 under forest canopies.

It is clear from this review that most work on sunflecks and R:F-r ratio has been done under temperate tree canopies, herbaceous agricultural crops, and tropical broadleaved forests. But none has been reported for the Afromontane coniferous forest.

1.3 Plant response to light and tolerance

1.3.1 Tolerance

In general, species can be classified into two main ecological groups based on their differential growth responses: shade tolerant or persistent species, and shade intolerant (light demanders) or gap requiring species (Denslow, 1980; Whitmore, 1984). Natural forests produce their own microclimates and there are many shade tolerant and light demanding shrubs, herbs, tree seedlings and saplings under the main canopy. The light demander species are further sub-divided into species, which are typical of the shade intolerant group and only regenerate in large gaps, where they complete their life cycle (pioneer species), and those species, which may be shade tolerant in some stage(s) of their development, but require gaps to reach maturity (gap species) (Denslow, 1980). Such a classification is an over-simplification, and in reality, species fall along a continuum in their light requirements (Wenger, 1984).

Table 1.3: R:F-r ratio estimated for shadelight beneath various vegetation canopies. Source: Morgan and Smith (1981a).

	Canopy	Skylight	R:FR ratio	Reference
(a)	CROPS			
	Wheat	Clear	0.49	Holmes and Smith (1979b)
		Overcast	0.59	Holmes and Smith (1979b)
	Maize	Clear	0.20	Yocum *et al.* (1964)
	Sugarbeet	Partially overcast	0.11-0.41	Holmes and Smith (1975)
	Tea	Overcast	0.09-0.15	Hadfield (1974)
(b)	BROADLEAVED DECIDUOUS WOODLAND			
	Beech	All conditions	0.16-0.64	Tasker and Smith (1977)
	Oak	Clear	0.12-0.17	Federer and Tanner (1966)
		Hazy	0.32	Federer and Tanner (1966)
		All conditions	0.37-0.77	Tasker and Smith (1977)
	Sweet Chestnut	Clear	0.12	Coombe (1957)
	Sugar maple	Clear	0.14-0.28	Vezina and Boulter (1966)
		Clear	0.08-0.11	Federer and Tanner (1966)
		Overcast	0.21	Federer and Tanner (1966)
	Birch	All conditions	0.56-0.78	Tasker and Smith (1977)
(c)	CONIFEROUS EVERGREEN WOODLAND			
	Spruce	Clear	0.33	Coombe (1957)
		Clear	0.15	Federer and Tanner (1966)
		Overcast	0.46	Federer and Tanner (1966)
	Red pine	Clear	0.47-0.76	Vezina and Boulter (1966)
		Clear	0.33	Federer and Tanner (1966)
		Partially overcast	0.55	Federer and Tanner (1966)
		Hazy	0.61	Federer and Tanner (1966)
	White pine	Clear	0.25-0.26	Federer and Tanner (1966)
		Hazy	0.49	Federer and Tanner (1966)
	Jack pine	Clear	0.32	Federer and Tanner (1966)
		Overcast	0.76	Federer and Tanner (1966)
(d)	TROPICAL RAIN FOREST			
	Montane	Bright	0.22-0.30	Stoutjesdijk (1972b)
		Overcast	0.77	Stoutjesdijk (1972b)
	Lowland	?	0.26	Stoutjesdijk (1972b)

A species is assigned to an ecological group usually based on its distribution spatially and temporally over microclimate (Denslow, 1980; Brokaw, 1985). Swaine and Whitmore (1988) proposed that, on the bases of seed germination requirements, a simple division of tropical forest tree species into two ecological groups, pioneer and non-pioneer (or climax) is possible. They suggested that seeds of pioneer species germinate only in canopy gaps and if exposed to full sunlight, whereas non-pioneer species have seeds that can germinate under forest canopy. Other authors, however, have reported differential germination (Raich and Gong, 1990) or establishment success (Brokaw, 1987) of different 'pioneer' species in canopy gaps of different size. Based on germination behaviour of 43 tree species native to the lowland forests of Malaysia, Raich and Gong (1990) showed that seeds of most gap-germinating species germinate to some extent in the forest understorey. They referred to the species that germinate best beneath a canopy opening as gap species, and those that germinate better in the forest understorey as non-pioneer species. Their gap species include both pioneer and non-pioneer species as suggested by Swaine and Whitmore (1988). Furthermore, Pompa and Bongers (1988) have used relative growth rate in response to gap light conditions as an index for shade tolerance. They have shown that pioneer species cannot persist under shade because of their negative net assimilation rate under light-limiting forest shade conditions. Investigations by other authors also revealed apparent differences in the regeneration of pioneer species in different parts of gaps, with some species establishing better than others in particular microsite conditions (Putz, 1983; Brandani *et al.*, 1988). More recently, Kennedy and Swaine (1992) have studied germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rainforest in Sabah, Malaysia and found that gap size did not affect germination, but germination was markedly increased by soil exposure or disturbance. Moreover, they found low seedling mortality both at larger gap size and in the absence of competition from advance regeneration. Taking all of the above together, it appears that assignment of species to ecological groups may not be simple, but gap size may operate through differential mortality at some stage in the development of a species.

1.3.2 Response to low PPF

There are several distinct types of morphological and physiological plant reaction to shade. These reactions have been reviewed and described in detailed by several workers (e.g. Fitter and Hay, 1987). The reactions can be summarized in brief:

1. Generally, the relationship between the rate of photosynthesis and PPF is different for leaves that have developed in sun versus shade, in that shade leaves display increased photosynthesis rates at low PPF.

2. Leaves developed in shade are frequently thinner, so that specific leaf area (the ratio of leaf area to leaf weight) is higher. Hence, more light energy can be captured per unit leaf weight.

3. The plant weight distribution between shoot and root parts is generally different for plants grown in shade compared to plants grown in the open. Shade plants often display relatively more shoot to root than plants grown at high PPF.

4. Plants grown in shade display more internode extension than plants of the same species grown at high PPF.

5. In addition to these features, shade plants differ in the light harvesting pigments proportions of chlorophyll a to b, which is part of the photosynthetic systems themselves.

Surprisingly, many plant species display consistent relative growth rate (R) over a wide range of PPF when they are grown from seed, and that this is achieved through adaptations in morphology (Corré, 1983b). The major adaptation to shade is the formation of thinner leaves resulting in higher specific leaf area (S). Another important adaptation is the decrease in root weight ratio (r) in shade. The dry matter not used in the root growth will be distributed to stems and petioles, and not to leaf blades, and thus does not contribute indirectly by saving carbohydrates since root respiration generally exceeds stem respiration (Corré, 1983a). Hence, on a unit weight basis the leaf weight ratio (w) can remain constant over a wide range of PPFs.

Equal LWR combined with increasing S leads to an increase leaf area ratio (F) and this relative increase in leaf area can compensate, at least partially, for a lower photosynthetic rate per unit of area. Grime (1965) claimed that many shade intolerant species show a more pronounced adaptations to low PPF than do shade tolerant species. Loach (1970) supported this view by an experiment which showed a greater adaptation of the F in *Liriodendron tulipifera* than in three shade tolerant tree species. He also cited examples of several shade tolerant species which showed less adaptation in terms of leaf thickness than did non-tolerant species.

Plants in the forest understorey habitat, exhibit a variety of photosynthetic characteristics that enable them to maintain a positive carbon balance under extremely low PPF (Boardman, 1977; Björkmann, 1981). Various authors have compared photosynthesis in shade tolerant and shade intolerant species. For example, shade adapted ecotypes showed appreciably lower photosynthesis per unit leaf area at high PPFs than sun adapted ecotypes grown at the same PPF in *Solidago virgaurea* L. (Björkman and Holmgren, 1963), *Rumex acetosa* (Björkman and Holmgren, 1966) and *Solanum dulcamara* (Gauhi, 1976). On the other hand, the initial slope of the light response curve of plants grown at low PPF was somewhat steeper in the shade adapted ecotypes (Björkman and Holmgren, 1963), but there was no significant difference in light compensation points, nor dark respiration. However, other workers found no difference in the apparent quantum efficiency and initial slope for a large number of tree species unless transfer from low to high light has taken place (Ramos and Grace, 1990; Riddoch, *et al.*, 1991).

Radosevich and Osteryoung (1987) cited Björkman (1981) who reviewed a number of studies in which herbaceous plants adapted to high-light habitats had lower maximum photosynthetic rates and lower light compensation points when grown under low light than clones of the same species grown under highlight. But, shade-grown plants still had higher light compensation points than shade adapted plants grown in deep shade. In general, shade-adapted plants do not appear to have as much capacity for response to high light, while some shade-adapted species even have lower maximum photosynthetic rates when grown in the sun than when grown in shade (Radosevich and Osteryoung, 1987). Photosynthetic characteristics of shade-tolerant tree species closely resemble those of shade-adapted herb; in that tolerant species can maintain a net carbon gain and are relatively efficient at light utilization at low light (Kramer and Kozlowski, 1960, in Radosevich and Osteryoung, 1987). The difference is, however, shade-tolerant tree species usually cannot acclimate easily to a sudden change in the light environment such as that following a complete canopy opening.

Rate of respiration is another possible difference between shade and sun plants at very low PPFs. Mohmoud and Grime (1974) reported for *Deschampsia flexuosa* (L.) Trin, *Festuca ovina* L. and *Agrostis temuis* Sibth (in order of decreasing shade tolerance) only negligible differences in light compensation points and in net photosynthesis at low PPF, based on whole plant dry weights. However, at PPFs less than the compensation point, the most shade tolerant species showed the smallest respiration losses, during a period of four weeks. Willmot and Moore (1973) report the same

phenomenon for *Silene alba* (Miller) E.H. Krause and *S. dioica* (L.) Clairv. grown at high and low PPF, with the shade tolerant *S. dioica* showing the smallest dark respiration rate. Loach (1967) found in *Populus tremula* L. much higher respiration losses when grown at low PPF than in some shade tolerant trees. Generally, seedlings of shade tolerant plant species could survive in absolute darkness much longer than intolerant species (Hutchinson, 1967). Moreover, a low respiration rate may lead to the maintenance of a higher soluble carbohydrate content, which gives the plant a higher resistant to fungal attack, a very important cause of death in shaded habitats (Vaartaja, 1962; Hutchinson, 1967).

1.3.3 Response to R:F-r ratio

It is clear from Section 1.2.1 above, that the forest understorey is characterized by a reduction in the R:F-r ratio. Plants appear to detect shade using phytochrome, a molecule which changes its state according to R:F-r ratio. A large number of studies on the physiological and ecological significance of spectral quality have documented the capacity of understorey plants to react to dense vegetation with changes in the pattern of morphological development, and much of this reaction is brought about through the change in Red:Far-red ratio (review by Smith, 1986).

i) Growth response

Studies on herbaceous plants show that species from open habitats are more responsive to R:F-r ratio than species which typically grow in vegetational shadelight (review by Smith, 1986). The effect of low R:F-r ratio on shade intolerant species in brief are:

1. promote stem elongation (review by Smith, 1986);
2. enhance dry matter allocation to stems (Corré, 1983a);
3. reduce total leaf area (McLaren and Smith, 1978), and
4. decrease leaf thickness resulting from a reduction in cell density of mesophyll and a reduction in air-space volume of spongy mesophyll (Child *et al.*, (1981).

In addition to the above characteristic a low R:F-r ratio also reduces chlorophyll mass per unit leaf area (McLaren and Smith, 1978), and chlorophyll a:b ratio (Lee, 1988).

The decreases in chlorophyll a:b ratios reflect differences in chloroplast ultrastracture, and greater allocations to Photosystem II compared to Photosystem I reaction centres (Glick *et al.*, 1985, in Lee, 1988). Thus, plant growth strategies and physiological processes are affected when grown under low PPF and R:F-r ratio (Lee, 1988).

There have been very few studies on the morphogenetic responses of tree seedlings to low R:F-r ratio (Morgan *et al.*, 1983; Kwesiga and Grace, 1986; Warrington *et al.*, 1989; Kamaluddin, 1991). Warrington *et al.* (1989) found in their experiment on relatively older materials of *Pinus radiata* D. Don. that apical dominance, stem height and diameter, and stem and needle dry weight markedly increased by a reduction in R:F-r ratio. Responses of tree seedlings other than stem elongation have been found to be differentially affected between pioneer and later successional species. Hoddinott and Hall (1982) found for *Phaseolus vulgaris* about 10% higher rates of photosynthesis under a R:F-r ratio of 0.7 compared to 4.7. Similarly, Kwesiga and Grace (1986) found higher rates of photosynthesis on shade leaves when grown in the R:F-r ratio typical of forest light, and proposed that there was a clear direct influence of spectral quality on the functioning of unit volume of leaf mesophyll. Also, higher photosynthetic rates were reported for *Pinus radiata* with low R:F-r ratio treatment (Warrington *et al.*, 1989). Moreover they found higher accumulation of dry matter under low R:F-r ratio and concluded that the increased dry matter did not result from enhanced photosynthesis but rather was a result of reduced mutual shading of adjacent leaves due to photomorphogenetically-controlled internode lengths. However, contrary to the above results, studies conducted on a number of herbaceous plants does not confirm the influence of R:F-r ratio (Corré, 1983a).

ii) Germination response

As discussed by Mayer and Poljakof-Mayber (1989), it is well established that seed germination in some species is affected by the presence or absence of light. In many species there exists light sensitized germination known as positive photoblastic (germination promoted by white light), whilst in other species germination is negatively photoblastic (Smith, 1975, in Morgan and Smith, 1981a). Photoblastic seeds have dormancy mechanism based on light quality especially the R:F-r ratio acting through the phytochrome system.

Taylorson and Bothwick (1969) claim that the increased R:F-r ratio under vegetation canopies relative to open condition inhibits germination in some species. They suggest

the possibility that in nature, phytochrome acts to detect exposure to light thereby inhibiting germination in seeds shaded by vegetation, allowing germination when vegetation is cleared or burned. Seeds of many species, however, show large variability in their germination behaviour.

Vázques-Yánes (1980) found that germination of two shade tolerant species was inhibited by the shade-light of rainforest canopy whilst germination was fully promoted when shade was filtered through a red narrow band-pass filter. Vázques-Yánes and Smith (1982) in another experiment of constant PPF with varying R:F-r ratio in four growth cabinets, found the germination of *Cecropia obtusifolia* and *Piper auritum* to be under photocontrol. However, *C. obtusifolia* seeds, germinated more slowly under low R:F-r ratio, but with sufficient time all seeds in all four chambers germinated. With *P. auritum*, some seed samples remained dormant under simulated dense canopies, and the effect of low R:F-r ratio was more drastic. The authors stressed that changes in light quality seem to be the only controlling mechanism of seed germination under natural conditions in relation to gap formation. Indeed it is the most efficient factor which permits germination to be timed precisely with gap formation when plants of many species may compete for establishment in a new open space.

1.4 Plant response to nutrient availability

The physiological characteristics that influence the ability of plant species to successfully exploit soil nutrients have been reviewed by Chapin (1980). In moderate to high fertility such as recently disturbed habitat, where a release of nutrients and other resources has occurred, an exploitative strategy allowing rapid uptake of and assimilation of nutrients confers a competitive advantage over less exploitative species. This type of strategy is found in competitors. The physiological traits that allow rapid exploitation of soil nutrients include: (1) high absorption capacity by roots (nutrient absorption per unit of root); (2) high photosynthetic rate; and (3) high respiration rate, which results in rapid growth. Maximum photosynthetic rate is sustained under high light conditions and maximum advantage is gained. In plants with these characteristics display sensitivity of photosynthesis to leaf nitrogen level, and growth rate declines with depletion of soil nitrogen, whilst photosynthesis and root absorption decline with tissue age. Other things being equal, such competitive species usually will outcompete other plants and maintain dominance as long as

nutrient levels remain high in the soil. However, if soil nutrients are depleted through time, these species will show signs of nutrient stress and will become less vigorous, and eventually stress-tolerant species may gain a competitive advantage (Chapin, 1980).

In contrast, the physiological characteristics that allow stress-tolerant species to compete successfully on infertile soils include: (1) high root absorption capacity; (2) low photosynthetic rate; (3) low rate of tissue production and growth, and (4) low rate of nutrient loss through senescence or leaching. Other adaptations that maximize nutrient retention include long-lived evergreen leaves, long-lived roots, effective translocation of nutrients between tissues, and traits that minimize foliar leaching by reducing water such as well-developed waxy cuticle and vertical leaf angle. In general, long-term adaptation to low nutrient supply is achieved by changes in demand for use of nutrients and by changes in root morphology and distribution (Fitter and Hay, 1987). Chapin (1980) also points out that many of the adaptive characteristics for low nutrient habitats (e.g. slow metabolic rates) are also adaptive for habitats deficient in other resources. For instance, shade-tolerant species, which show the conservative traits adaptive to low nutrient, gain a competitive advantage and eventually dominate, in the years following a disturbance, as the canopy progressively becomes more dense and light availability in the understorey becomes reduced (Grime, 1979, in Radosevich and Osteryoung, 1987).

1.5 Forest harvesting practices

Understanding the factors that promote, prevent, or delay seed germination in different environments is essential to understand why a species regenerates and subsequently survives, or does not regenerate at all. Seed germination may be influenced by a wide variety of both endogenous and exogenous factors (e.g. Smith, 1986; Mayer and Poljakoff-Mayber, 1989; Hart, 1991). White (1983) and Vázquez-Yanes and Orozco-Segovia (1984) have reviewed environmental influences on the germination of tropical tree seeds. Light, temperature and moisture are particularly important and are affected when a gap or a clearing is formed in closed-canopy forest (White, 1983). Therefore, gap formation should influence seed germination.

The crucial environmental characteristics of seedling microsites are very different from those that will govern the development of a tree after its shoot and roots have extended to a few centimetres above and below the soil-air interface. Each species is adapted to a range of microsites. This range is wider for some than for others but none are adapted to the full range (Smith, 1986). Successful germination depends largely on the nature of the spot where the seeds are deposited. Three basic requirements are important for success in natural regeneration. These include: (1) an adequate supply of seed, (2) a suitable seedbed, and (3) an environment compatible with germination and survival (e.g. Smith, 1986).

1.5.1 Silvicultural systems

Several authors have defined and described in detail a range of forest harvesting practices (silvicultural systems) available (e.g. Smith, 1986; de Graaf, 1986; Walstad *et al.*, 1987; Tappeiner II and Wagner, 1987; Matthews, 1989; Hart, 1991). Some of these authors have described silvicultural systems as applied in some tropical moist/rainforests (e.g. de Graaf, 1986; Matthews, 1989), but none for the Afromontane coniferous forests. Silvicultural vegetation management practices include harvesting, site preparation, stand release, and timber stand improvement. These practices are based on ecological principles described earlier. Harvesting, by its nature, affects existing plants and also sets the stage for subsequent development of vegetation. It is not the intention of this section to review the silvicultural systems available, but only a brief overview of even-aged systems, will be given due to their relevance to the present study.

Even-aged silvicultural management regimes generally produce the most profitable yield of desirable wood, particularly for species naturally adapted to even-aged conditions. This approach involves clearcutting, seed-tree, or shelterwood silvicultural systems of harvesting and regeneration. These systems have been successfully applied to a wide range of conifer species (Walstad *et al.*, 1987). Of the three systems, clearcutting is conceptually the simplest way (removal of the entire stand in one cutting and complete replacement of old stands in better sites). Regeneration is obtained artificially, or by natural seeding from adjacent stands, or from seed on the site (from trees cut in the clearing operation, or seeds stored in the forest floor). There are, however, instances where the site may be below-average, or where certain species may require some sort of shading, in which natural regeneration by seed-tree and shelterwood systems of harvesting is preferred.

i) Clearcutting systems

Clearcutting with natural regeneration has been in operation in Germany for several hundred years, and in Europe received serious attention from about the middle of the eighteen century (Matthews, 1989). Today, it is the most widely used silvicultural system in the world, in its various forms (Matthews, 1989). It is employed for the loblolly pine stands of coastal South Carolina, USA (Lotti, 1961, in Smith, 1986), the species of pines that have serotinous cones e.g. jack pine and lodgepole pine in USA (Smith, 1986) the maritime pine forests of the Landes in south-west France (Lanier, 1986, in Matthews, 1989). One variant is patch felling to produce mixed stands of Douglas fir with its associate Western hemlock, together with western red cedar, Alaska yellow cedar, some lodgepole pine, red alder, and bigleaf maple on Vancover Islands in British Columbia (Matthews, 1989).

The prospect of success with natural regeneration after clearcutting and the ways of securing it depend much upon the source and the agency of dispersal of the seeds. Clearcutting with natural regeneration from adjoining stands has been applied to conifers in Europe (Matthews, 1989). These may take the form of strip-like clear cuttings made either by progressive fellings or by fellings in alternate strips. With such an approach, however, the agency of dispersal is important. Pioneer species, particularly those with winged seeds in the temperate zone are best adapted to this kind of silviculture, while in the tropics where it is less windy or seeds are not winged, birds and other animals may play a more important role (Smith, 1986). Regeneration of clearcut stands may also depend upon seedbank in which a fraction of the dispersed seed survives in a dormant condition in the soil (Hutchings, 1986).

Clearcutting with natural regeneration is usually associated with comparatively extensive, low-investment silviculture (e.g. Matthews, 1989). However, the prospect of success with natural regeneration after clearcutting and the ways of securing it vary widely depending upon the source and means of dispersal of seeds (e.g. Smith, 1986).

ii) Shelterwood systems

The shelterwood system is the establishment of a new, essentially even-aged, stand from the release, (typically in a series of cuttings) of new trees started under the old stand. The essential characteristic of the system is that the new stand is established naturally before the old one is removed. The system may involve a series of three

different kinds of cutting: (1) a preparatory cutting; (2) seed cutting; and (3) one or more removal cuttings to release the newly established crop or to harvest the remaining old trees (Smith, 1986).

The shelterwood and the seed-tree methods can be adapted to wide range of ecological conditions and management objectives. All the variants have in common the retention of the seed source on the site until the new stand is established. Even if regeneration fails after one good seed crop, it is possible to wait for the next, which costs nothing except repeated site preparation. The degree of exposure and treatment of the forest floor can be varied to favour the regeneration of species with different shade tolerance and successional status.

The seed-tree method, for example, is used for light-demanding species with seed that is easily dispersed, mostly by wind, for such species as loblolly, longleaf, slash, and shortleaf pines in the southern USA, and ponderosa pine and western larch in the Western USA, *Pinus roxburghii* (Chir pine) in northern India and Pakistan. The seed-tree method is not applicable for shallow rooting species, since windfirmness is a primary consideration in choosing seed trees (Matthews, 1989). In many of these forests, the thick layer of undecomposed needles and competing vegetation is removed by controlled burning.

In considering the regeneration of forest stands emphasis is traditionally and logically placed on silvicultural systems (the pattern by which the existing stand is removed) to provide sufficient growing space. However, such emphasis on harvest cutting should not obscure the fact that regeneration may also depend on measures to dispose of debris, reduce the competition of unharvested vegetation and prepare the soil for the new trees (e.g. Alexander, 1984). Therefore, site preparation may be more crucial in the establishment of regeneration than the method of felling. Furthermore, while many species can be reproduced by several different methods of cutting, the general program of site preparation is dictated by the characteristics of species and site. The important objective is to prescribe and create environmental conditions conducive to the establishment and growth of the desired species. The more important of site preparation treatments include disposal of the logging waste and treatment of the forest floor and competing vegetation.

1.5.2 Site preparation

Dense concentrations of logging waste left by harvesting operations, in addition to being a hazard and impediment to forest fire control, often hinder the establishment of regeneration. In such places, advance regeneration is buried or crushed and the establishment of new seedlings is prevented by the shade (DeByle, 1981; Smith, 1986).

Vegetation has long been seen to affect regeneration (McNeill, 1945). It is thought that if seedling germination of the desired tree species occurs concurrently with vegetation colonization, the tree seedlings will be able to compete effectively (e.g. Smith, 1986). However, an established cover will affect the chances of germination to varying degrees. Tall, dense grass is often reported to compete with tree seedlings enough to reduce survival (Robertson, 1976). Hence, ground preparation that exposes mineral soil following logging disposal may improve conditions for regeneration. Moreover, horizontally orientated forest floor materials, such as thick coniferous litter, tend to inhibit penetration of seeds into moist substrata (Robertson, 1976; Smith, 1986). Thus, the preparation of seedbeds may be necessary, and ordinarily involves treatment of the forest floor, which is the layer of unincorporated organic matter that lie on the mineral soil.

Some scarification of the mineral soil and reduction of competing vegetation may be accomplished during logging and disposal of logging waste. However, such disturbance seldom results in very complete scarification and exposure of substantial amount of mineral soil, or eradication of much sprouting vegetation. Deliberate measures such as prescribed burning and mechanical site preparation are, therefore, necessary to create the appropriate environmental conditions for natural or artificial regeneration. Prescribed burning can be used to reduce or eliminate logging waste, unincorporated organic matter of the forest floor or low, undesirable vegetation, thereby exposing the mineral soil (Matthews, 1989). Alternatively, mechanical site preparation which involves removal of the logging waste, undesirable vegetation and subsequent scarification of the litter may be used (e.g. Smith, 1986).

Many authors have found that surface disturbance increased regeneration density when compared to undisturbed controls, for most conifer species (e.g. Noble and Alexander, 1977; DeByle, 1981; Benson, 1982), and for dipterocarp rainforest (e.g. Kennedy and Swaine, 1992). Mineral soil can be exposed by burning and mechanical

scarification. The details of the application vary according to the species and objectives of treatment.

1.6 Objectives of the study

The general objective of this study is to identify the factors affecting the regeneration of *J. procera* and *A. gracilior* in relation to management practices and responses of seedlings to light and nutrient supply. The three fundamental questions this work sets out to answer are: (a) is canopy opening or ground disturbance effective in enhancing the regeneration of these species?, (b) do these species respond similarly to similar seed germination treatments?, and (c) how do seedlings of these species respond to light and nutrient availability?

The responses observed from the field experiments can provide confirmation of the potentially richer data set obtained from experimentation in controlled glasshouse and growth room environments. Hence, in order to achieve its objective this thesis contains a blend of these approaches.

Specifically, the study aims at:-

1. characterising the forest understorey light, air temperature and soil moisture environment;

2. assessing the relationships between microsite conditions and the number and distribution of naturally occuring *J. procera* and *A. gracilior* seedlings, and examining the viability and germination of the soil seedbank of the undisturbed forest understorey;

3. investigating the effects of ground preparation on the germination and/or natural regeneration following clear cutting and timber extraction;

4. exploring the effects of pre-germination treatments and simulated canopy light on seed germination;

5. characterising the effects of light and nutrient supply on the growth and development of seedlings by growing them in simulated light regime of

understorey habitats, disturbance, and forest clearing in a glasshouse and relate to the seedling growth under field condition, and

6. investigating whether the Afromontane conifers are capable of using the Red:Far-red ratio as a signal of shade.

CHAPTER 2

A Re-appraisal of *Juniperus procera* and *Afrocarpus gracilior*: Historical and Management Background; and Description of the Field Study Area.

This chapter is divided into two sections. Section 2.1 briefly reviews the systematic position, distribution and status, ecological amplitude, silviculture, and economic significance of the species. Section 2.2, is concerned with the description of the field study area, Arba-gugu forest. It provides basic information on terrain, geology and soils, climate, and natural fauna and flora.

2.1 A re-appraisal of the species

2.1.1 Scientific recognition of the species

i) *Juniperus procera* Hochst. ex Endl. (Cupressaceae)

Taxonomically, *J. procera* is included in the arborescent multiseed *Juniperus* section *Sabina* (Mill) Spach characterized by small scale-leaves, which are decurrent and decussate (Farjon, 1992). Although the initial discoverer of the species remains uncertain, it is believed that the name *J. procera* was first published by Endlicher (1847) when he labelled plant specimens collected by W. Schimper from Ethiopia in 1838. Endlicher compared it with its close allies *Juniperus foetidissima* Willd. and *J. excelsa* M. Bieb., and considered it to be distinct.

The affinity with *J. excelsa* which was first expressed by Endlicher (1984) (in Farjon, 1992), was emphasized by Exell & and Wild (1960) in *Flora Zambesiaca* where they suggested *J. procera* to be a variety of *J. excelsa*, but retained its specific status (cited in Farjon, 1992). Kerfoot, who at first accepted the populations on the eastern coast of the Red Sea as *J. procera*; subsequently called them as *J. excelsa*. The name *Juniperus procera* was then considered synonymous with *Juniperus excelsa*. Some other species including *Juniperus polycarpos* C. Koch. and *Juniperus marcropoda* Bioss were also included in *Juniperus excelsa* (Khalinque and Perveen, 1977; Quraishi *et al.*, 1977; Javeed *et al.*, 1980). Kerfoot (1966) suggests that *J. procera* is

phytogeographically a well separated species which has migrated by way of the western mountains of the Arabian Peninsula into Africa during the Miocene-Pliocene (cited by Farjon, 1992). However, Farjon (1992) cited Adams (1990) who has convincingly shown that *J. procera* is properly regarded as a separate species on chemotaxonomic grounds. He separated the species from *J. excelsa* based on its smaller cones with fewer seeds, as well as its more acute leaves. These are differential characters which are remarkably constant throughout its range.

ii) *Afrocarpus gracilior* (Pilger) C. N. Page (Podocarpaceae)

The history and the taxonomic status of the *Afrocarpus gracilior* (which used to be known as *Podocarpus gracilior* Pilger) is complex but interesting. The adoption of *Afrocarpus* at generic rank and the grouping of *Afrocarpus gracilior* and other five species into this genus was first proposed by Gaussen (1974). Despite his suggestion, however, all were invalidly published (Table 2.1). *Afrocarpus* C. N. Page, a genus of three or more species all endemic to the African continent, has always been in a somewhat anomalous position in the Podocarpaceae (Page, 1988). The species were treated simply as *Podocarpus*, but modern taxonomic treatments define the genus *Podocarpus* as the female fruit having fleshy receptacles, which the species of *Afrocarpus* do not. Because they lack this character, they resemble *Retrophyllum* and most species of *Nageia*, but differ in vegetative characters from both these genera quite clearly, which seem much more akin to those of *Podocarpus*. Ferre *et al.* (1975) describes the genus *Afrocarpus* as lacking the unusual fine parallel venation of *Nageia* and the small, curiously rotated leaves of *Retrophyllum*, whilst also differing from *Podocarpus* in seedling morphology and anatomy (cited by Page, 1988).

Moreover, *Afrocarpus* species differ in cytology from other allied genera in that they have $n = 12$ chromosomes, differing from *Retrophyllum* with $n = 10$, *Nageia* with $n = 13$ and the African *Podocarpus* with $n = 11$ (cited by Page, 1988). *Afrocarpus* also differs from *Podocarpus* by having mostly amphistomatic leaves (Page, 1988).

Currently, Page (1988) places the six species into the genus *Afrocarpus* based on their vegetative and reproductive features (Table 2.1).

Table 2.1: Past views, synonyms and current taxonomic treatments of species of the genus *Afrocarpus*. Years of the old taxonomic treatment are given in parenthesis. Source: Page (1988).

	Past views	Current treatment
1	*Taxus falcata* Thunb. (1800)	*Afrocarpus falcata* (Thunb.) C. N. Page
	Synonyms:	
	Podocarus falcatus (Thunb.) R. Br. ex Mirb. (1825) *Nageia falacata* (Thunb.) O. Kuntze (1891) *Decussocarpus falcatus* (Thunb.) de Laub. (1969)	
2	*Podocarpus gracilior* Pilger (1903)	*Afrocarpus gracilior* (Pilger) C. N. Page
	Synonyms:	
	Decussocarpus gracilior (Pilger) de Laub. (1969)	
3	*Podocarpus mannii* Hook. f. (1864)	*Afrocarpus mannii* (Pilger) C. N. Page
	Synonyms:	
	Nageia mannii (Hook. f.) O. Kuntze (1891) *Decussocarpus mannii* (Hook. f.) de Laub. (1969)	
4	*Podocarpus usambarensis* Pilger (1903)	*Afrocarpus usambarensis* (Pilger) C. N. Page
5	*Podocarpus Dawei* Stapf (1917)	*Afrocarpus Dawei* (Pilger) C.N. Page
6	*Podocarpus gaussenii* Woltz (1969)	*Afrocarpus gaussenii* (Pilger) C.N. Page

2.1.2 Morphological features

J. procera is a straight evergreen, usually dioecious, more seldom monoecious tree of 20-45 m tall and up to 2 m d.b.h. (Fig. 2.1). Crown: conical in outline when young, more spreading when older. Bark: smooth at first, very soon with papery flakes, purplish, on older trees fibrous, deeply longitudinally furrowed, peeling in long, narrow strips, pale brown or grey brown. Leaves: on young plants in threes, subulate, spine-tipped, epistomatic; mature foliage of decussate scale-like leaves varying with age of the individual, abaxial gland elliptic, amphistomatic. The description of morphological and reproductive features of *J. procera* are given in detail by Lewis (1960), Jansen (1981) and recently by Farjon (1992).

A. gracilior is a tall evergreen, columnar, dioecious tree, with long, clean and cylindrical trunk (Fig 2.2). Different heights between 30 to 45 m (Lewis, 1960; Bryce, 1967) and variability in diameter between 2 to 3 m have been reported

Figure 2.1: Photograph showing the size and form of the stem and nature of bark of *J. procera* trees in Arba-gugu forest, Ethiopia. Note the fluting and the spiral grain stem.

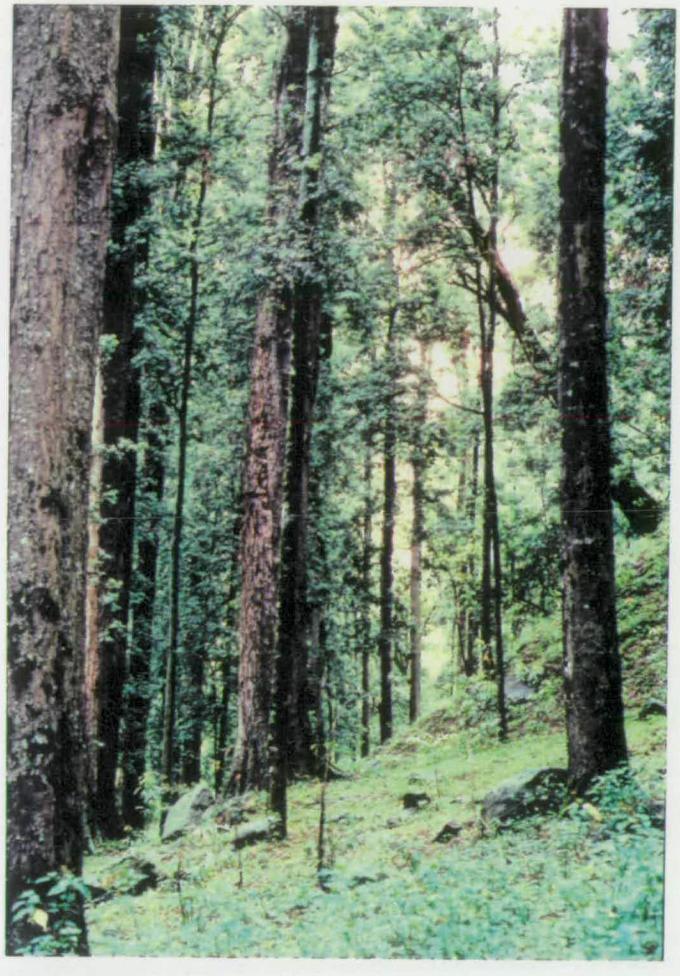

Figure 2.2: Photograph of pure *A. gracilior* forest stand in Din-din forest, Ethiopia, at an altitude of 2200 m, showing the form of trees and the forest environment. Note the proportion of young trees and poor ground vegetation.

(Chaffey, 1979). The bark is thin, rather smooth and greyish-brown to dark-brown in colour, when mature it exfoliates in rectangular to irregular flakes. Twigs slightly angled by the decurrent leaf scars, green in colour; buds obtuse, 0.1 cm long (Lewis, 1960).

2.1.3 Distribution and status

i) Geographical range

Juniperus procera occurs in the mountainous regions and highlands of East Africa. The species is mainly distributed in NE Sudan near the Red Sea, in the Ethiopian highlands, Djibouti, Somalia, Kenya, Uganda, Tanzania, in extreme eastern Zaire, Malawi and northeastern Zimbabwe, and in the mountains alongside the shore of the Red Sea in Saudi Arabia and Yemen (Kerfoot, 1966; Kelecha, 1979, Farjon, 1992; Pohjönen and Pukkala, 1992) (see also Fig. 2.3).

A. gracilior extends from Ethiopia in the north to Zaïre in the South (Ethiopia, Uganda and Zaïre) (Gaussen, 1974) (see Fig. 2.3). Between these limits the species has been reported from most of the Afromontane region on the eastern side of Africa (White 1983).

ii) Population status

The occurrence of *J. procera* forests is believed to have been continuous in many regions in the past. It has been estimated that *J. procera* forests covered about 200,000 ha in Ethiopia in 1955 (Jones, 1989) and 130,000 ha in Kenya early in this century (Gardner, 1926), including both pure and mixed forms. The present population status of the species in the east African highlands suggests that present *J. procera* populations are mere vestiges of the former extensive ones. At present a single tree is reported to survive in the southern extreme range of Inyanga mountains in Zimbabwe, whilst in Zaire and Malawi only a few trees exist in the forest population (Hall, 1984; FAO, 1986). A review of the literature clearly demonstrates that without swift positive human intervention the currently dwindling population may soon become extinct.

Within the range of *A. gracilior*, four parts are identifiable based on a combination of geographical pattern and environmental factors. The most typical pattern corresponds

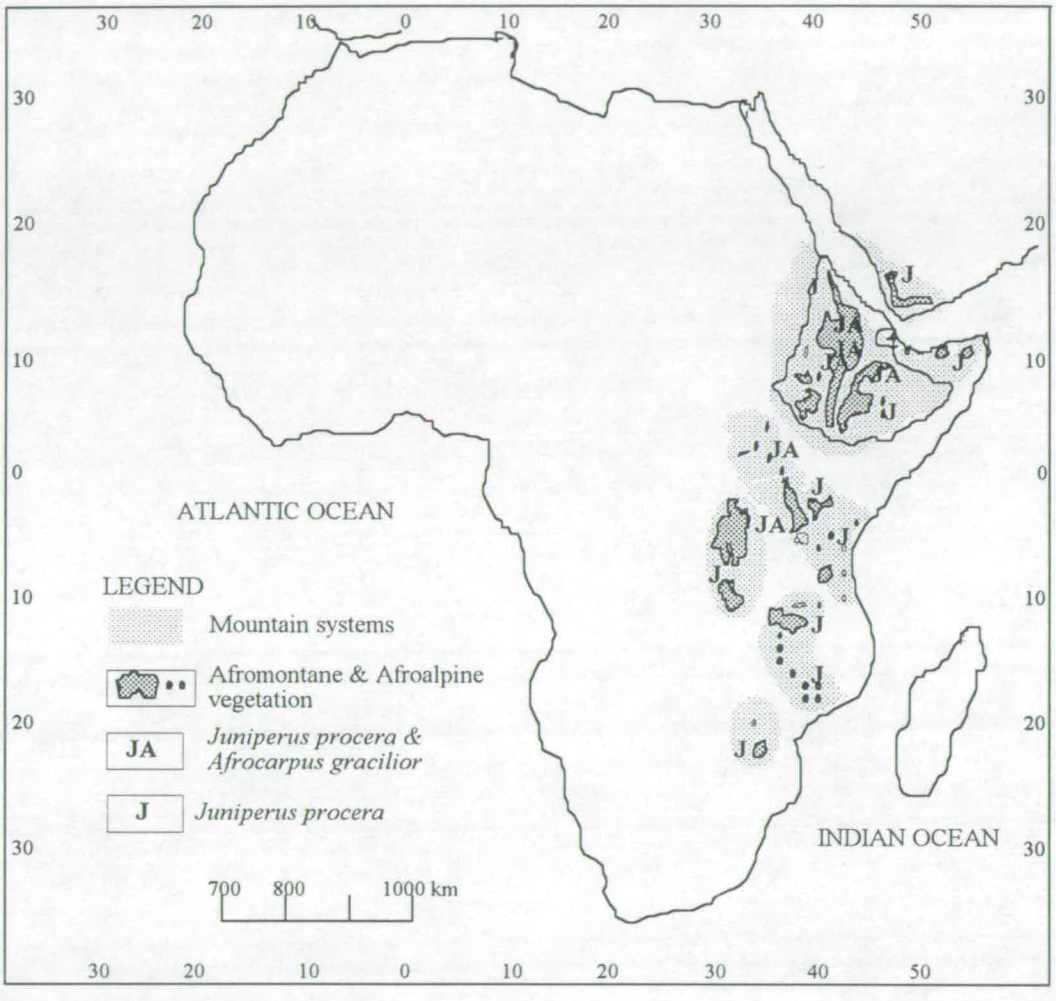

Figure 2.3: Map showing ecological distribution of *Juniperus procera* (J) and *Afrocarpus gracilior* (A) within the Afromontane forests. Shaded areas indicate regional mountain systems within which the Afromontane and the Afroalpine vegetation are distributed. The letters 'A and JA' indicate the extent of the species distribution. Reproduced from White (1978) and Farjon (1992).

to regions (Ethiopia, Kenya, Uganda, Rwanda, Tanzania, Zaïre) where the species was widely known as *P. gracilior* or *P. usambarensis* var. *usambarensis* (Melville, 1954). However, the most highly stocked areas are in Ethiopia (nothern Bale, Harerghe and Shoa forests) with up to 32 stems (≥30 cm dbh) ha^{-1} (Chaffey, 1979). It is probable that many more localities once had the species in abundance though figures to support this are unavailable.

2.1.4 Causes of decline

Generally, *J. procera* can withstand extremes of climatic fluctuations (Gardner, 1926; Hall, 1984; FAO, 1986). However, these forests have not escaped the pressures that have led to tropical forest destruction world-wide and agricultural activities have been responsible for extensive forest clearance. The imbalance between sawnwood need and home grown sawnwood supply, and the escalation of demand for fuelwood has threathened the existence of *J. procera* and *A. gracilior* forests. Unmanaged over-expliotation of these most sought-after species during the past several decades caused a sharp decline in the extent of the species throughout their range (Hall, 1984; FAO, 1986; Jone, 1989; Negussie *et al.*, 1991). Moreover, continuous and increased overgrazing and destruction by fire, particularly *J. procera*, have also contributed to the gradual decline of the species to the verge of extinction (Gardner, 1926; Hall, 1984).

For instance, in those areas of Ethiopia where forest explotation has already taken place, but where some form of forest cover still exists it is in the category of "disturbed high forest". Generally the tallest, the good form and the biggest trees have been removed in an exploitation often referred to as "high grading". What was left behind was the oldest, the poorest and the damaged trees, that nobody wanted. In other words, more often only the trees of the poorer phenotype and genetic background were left. Often the area has been burned and over 50% of the forest products left to rot or remain as "stag heads". Finally the area has been cultivated or become a permanent grazing ground (Fig. 2.4, 2.5) or in a very few instances has been reforested mainly with exotic species (Fig. 2.6).

Apart from cultivating and over grazing other damage done to the forest by the local people includes stripping the bark of *J. procera* trunk for making beehives and for roofing material in place of grass thatch (Fig. 2.7).

Figure 2.4: Representative scene of *J. procera* and *A. gracilior* forest under continuous exploitation in Arba-gugu, Ethiopia. a: Valley bottoms have been cultivated for several years. Encroachment of slopes by crop farmers (foreground) and cattle browsing after heavy timber explotation in the background. b: logged, disturbed and heavily grazed site (note browzed young trees of *A. gracilior* under itself and *Hagenia abyssinica*).

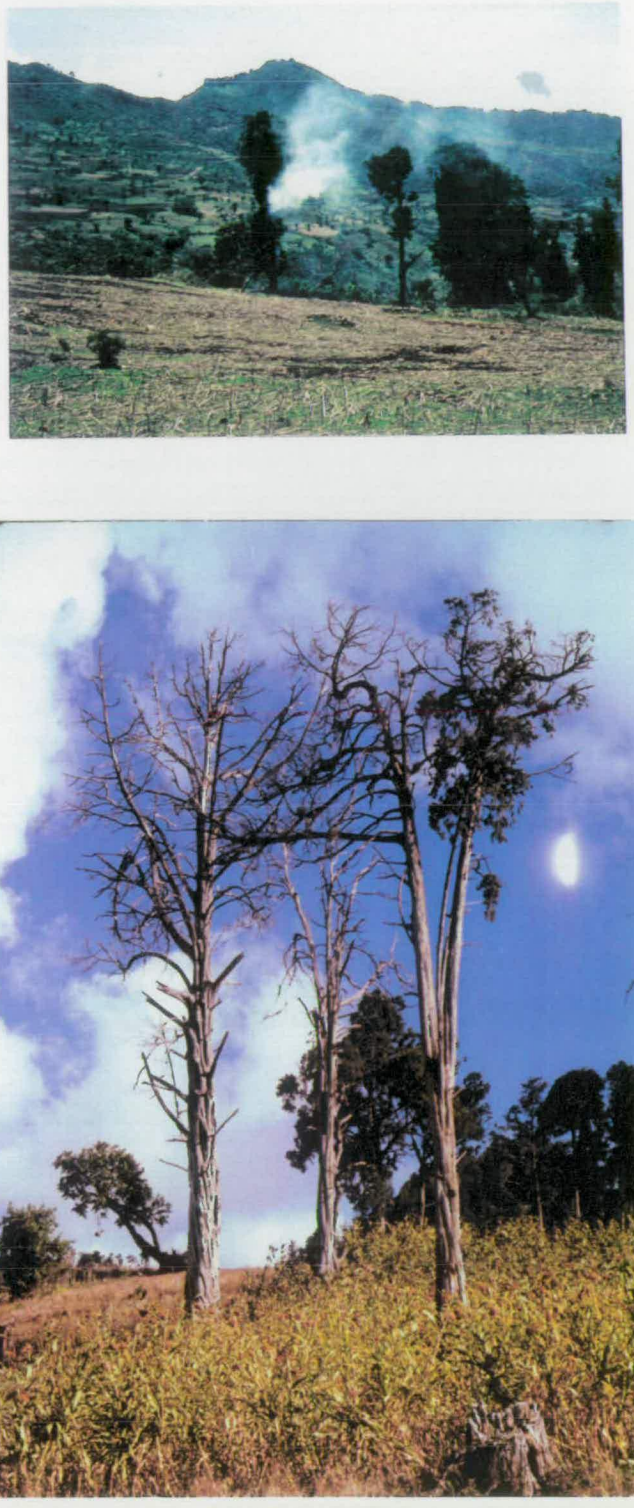

Figure 2.5: Example of conversion of *J. procera* and *A. graclior* forest into agricultural land in Arba-gugu. Unutilized overaged and poorly shaped *J. procera* are bound to vanish in a field of sorghum.

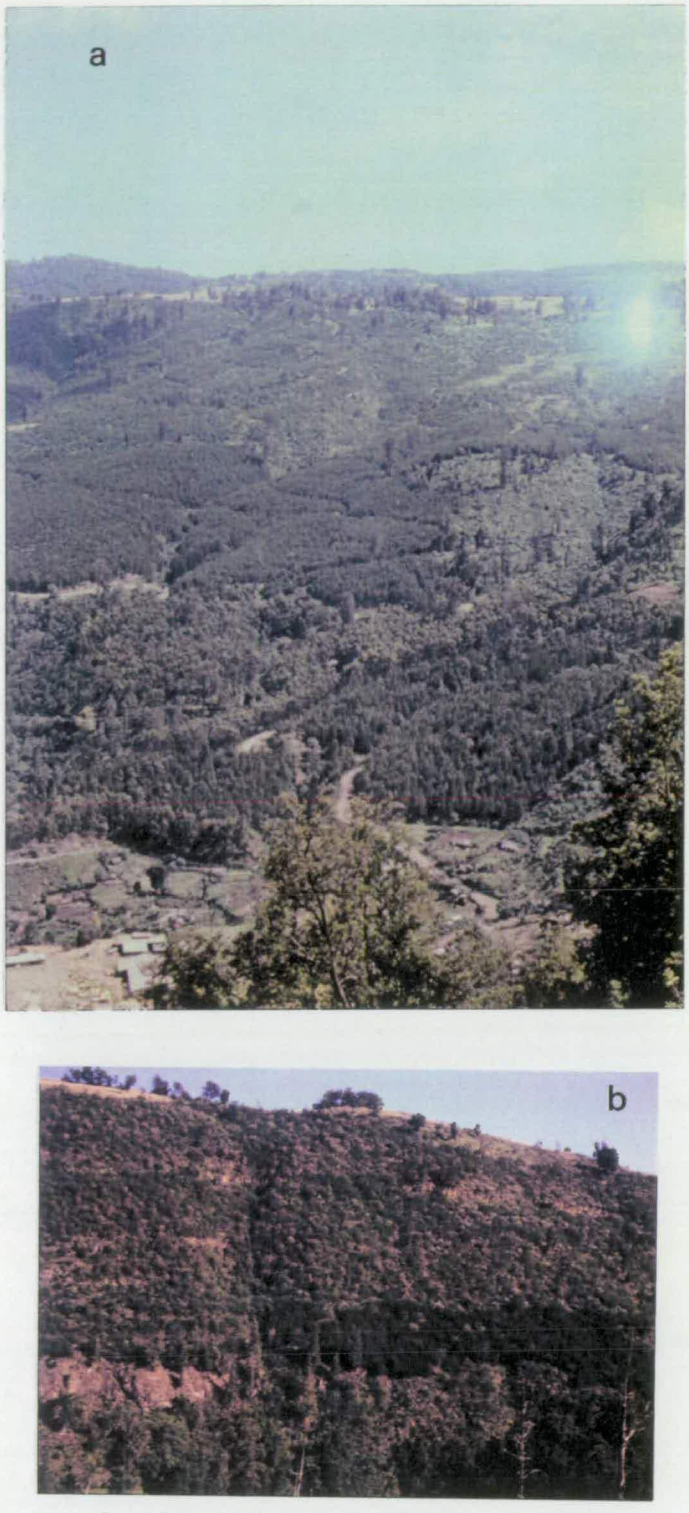

Figure 2.6: Example of reforestation programme converting *J. procera* and *A. graclior* forest into exotic species following timber exploitation in Arba-gugu forest. Main species planted include *Cupressus lusitanica* and *Pinus patula*. a: Large scale reforestation programme. Government sawmill in the valley bottom. b: Degraded forest land by fire and over grazing with small area planted following timber exploitation on very steep slope.

Figure 2.7: Example of stripping the bark of *J. procera* trunk for making beehives and for roofing material in place of grass thatch

2.1.5 Ecological amplitude

i) Relationships with physical environmental factors

J. procera, although mostly confined to high altitudes, occurs over a wide range of altitudes. In its east African range it extends from 800 to 3,600 m (Hall, 1984) but mostly grows on the drier slopes of mountains between an altitudinal range of 1,800 and 2,900 m, occasionally descending to 1000 m (White, 1983). A possible association of the tree with wind exposed aspects has been noted in areas with less than 700 mm mean annual rainfall (Hall, 1984).

J. procera occurs naturally in areas underlain by rocks as diverse as limestones, sandstones, gneisses and granites of the basement complex and basalts. Well documented information on the soil type requirement of the *J. procera* is scarce. Most frequently it occurs on steep slopes where many surface rocks dominate on shallow soils, varying from dark-red to blackish brown. Normally soils with deep surface humus accumulation impede natural regeneration.

J. procera's distribution is critically influenced by three climatic factors namely, rainfall, temperature and solar radiation (Gardner, 1926; Jansen, 1981; FAO, 1986). *J. procera* grows in areas where rainfall is extremely low and erratic with a mean annual rainfall ranging between 400 and 1,200 mm with a pronounced dry period. The distribution of the species is closely related to rainfall. It cannot compete with vigorously growing broad-leaved species under natural condition where the average rainfall is over 1,250 mm (Gardner, 1926; Jansen, 1981; Hall, 1984; FAO, 1986). Despite the complete absence of the species in rain forests, it can be grown in high rainfall areas if broad-leaved species are regularly kept under control (Hall, 1984). It competes well and becomes a dominant tree in areas with less than 600 mm mean annual rainfall. In east African Highlands, *J. procera* forests occur in areas with a mean annual temperature of less than 19 ^{o}C (Hall, 1984). High insolation is an important characteristic of *J. procera* forest areas. It is a light demanding species and easily succumbs if over-topped by neighbouring trees (Gardner, 1926).

The altitudinal range of *A. gracilior* varies from about 1500 m to over 3,000 m (Mount Kenya). Herbarium and published notes suggest that the highest elevations are reached at low latitude. In its Ethiopian range, it occurs between an altitudinal range of 1,500 and 2,800 m. *A. gracilior* grows on a wide range of soils derived from

various parent rocks particularly from precambrian metamorphic and volcanic basic rocks. The association with volcanic rocks in East Africa probably reflects the prevalence of the high ground formed by volcanic activity rather than the physical and chemical properties of soils associated with the species, as in the case of *J. procera* (Hall, 1984).

Relationships of *A. gracilior* with environmental factors are only broadly indicated in the existing literature (Battiscombe, 1936; Lind and Morrson, 1974; White, 1983). Based on the data assembled from the nearest meteorological stations where *A. gracilior* occur, the mean annual rainfall varies from 800 to 1,700 mm with about 6 to 11 wet months (White, 1983).

ii) Phytosociology

White (1983) designates *J. procera* in the single-dominant Afromontane forest (SDAMF). It also occurs as an emergent in scrub forest and evergreen bushland where the annual rainfall is as low as 650 mm (Hemming, 1966, in White, 1983). In some places the trees are much shorter with numerous and dense bushes, forming a thicket. *J. procera* in the SDAMF is a dominant tree of about 20 to 30 m high, with relatively open canopy in drier sites (Fig. 2.8), reaching up to 45 m in height, with dense canopy in most favourable sites. More often, it is mixed with *Olea europea* ssp. *africana* (Table 2.2). Generally the undergrowth is poorly developed.

In more favourable sites where rainfall is higher *J. procera* is mixed with *A. gracilior* (Fig. 2.9) but becomes the dominant species on the ridges and at higher elevation on drier sites (Fig. 2.10) and at lower altitudes on yet drier sites where the rainfall does not exceed 1,100 mm (Fris *et al.*, 1982). At the upper limit it is often mixed with *Hagena abyssinica* and *Hypericum revolutum.* At lower elevation and sheltered valleys *A. gracilior* is the dominant conifer. Its occurrence in the undifferentiated Afromontane forest (UAMF), according to White (1983), is as an early colonizer after fire. This forest type, usually, contains a variety of hardwood species (Table 2.2).

White (1983) designates *A. gracilior* in the undifferentiated Afromontane forest (UAMF) vegetation. This forest type is usually shorter than Afromontane rain forest (AMRF) and usually replacing it at comparable altitudes on the drier slopes and at higher altitudes on the wetter slopes. It also occurs below AMRF on some mountains. The main associated species with *A. gracilior* in (UAMF) are listed in Table 2.2. In

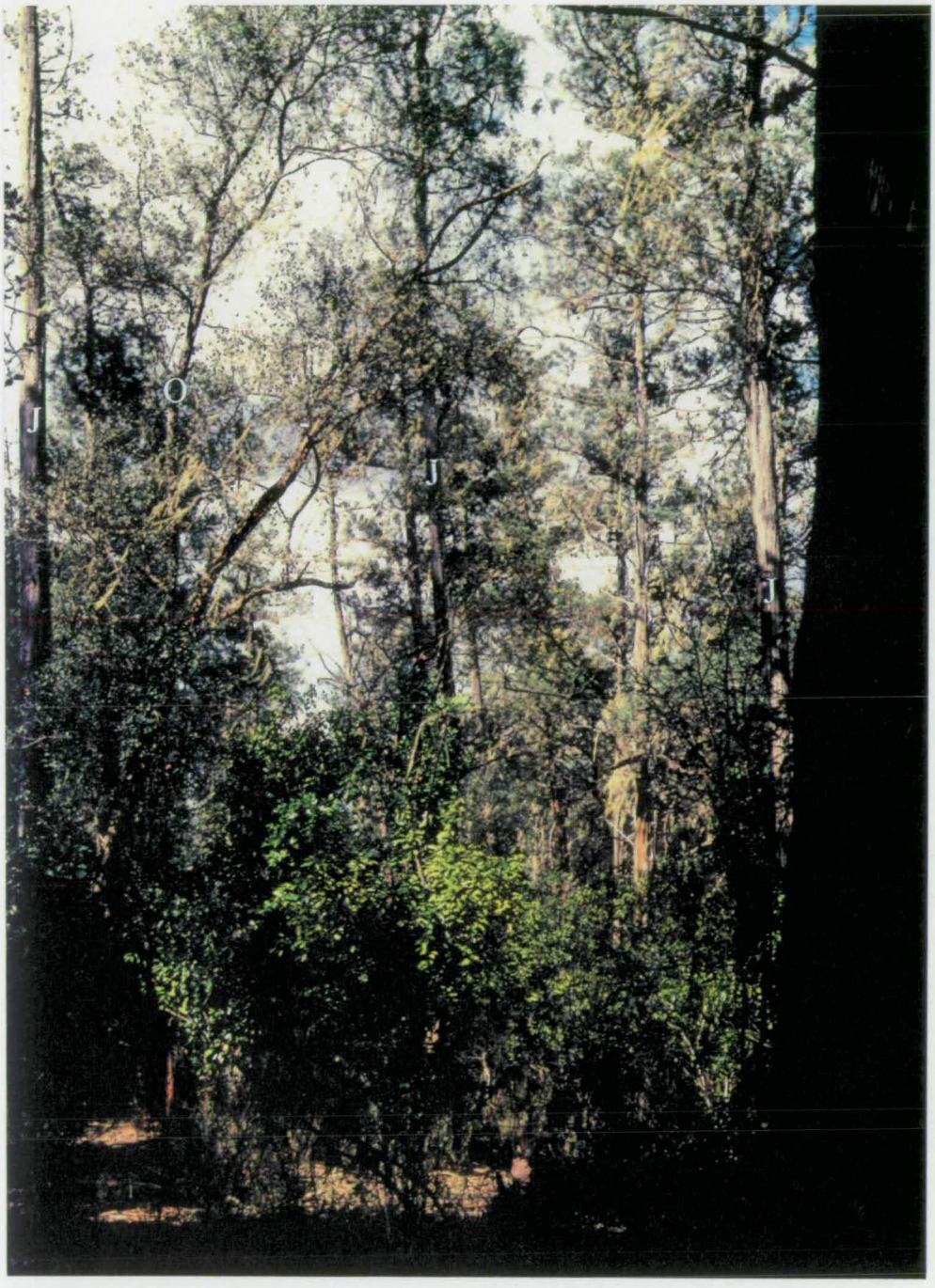

Figure 2.8: Photograph of *J. procera* forest stand in Arero forest, Ethiopia, at an altitude of 1700 m, showing the form of trees and the forest environment in relatively hotter and drier climate. Note the openess of the canopy and the canopy species: *J* = *J. procera* and *O* = *Olea europea* ssp. *africana*.

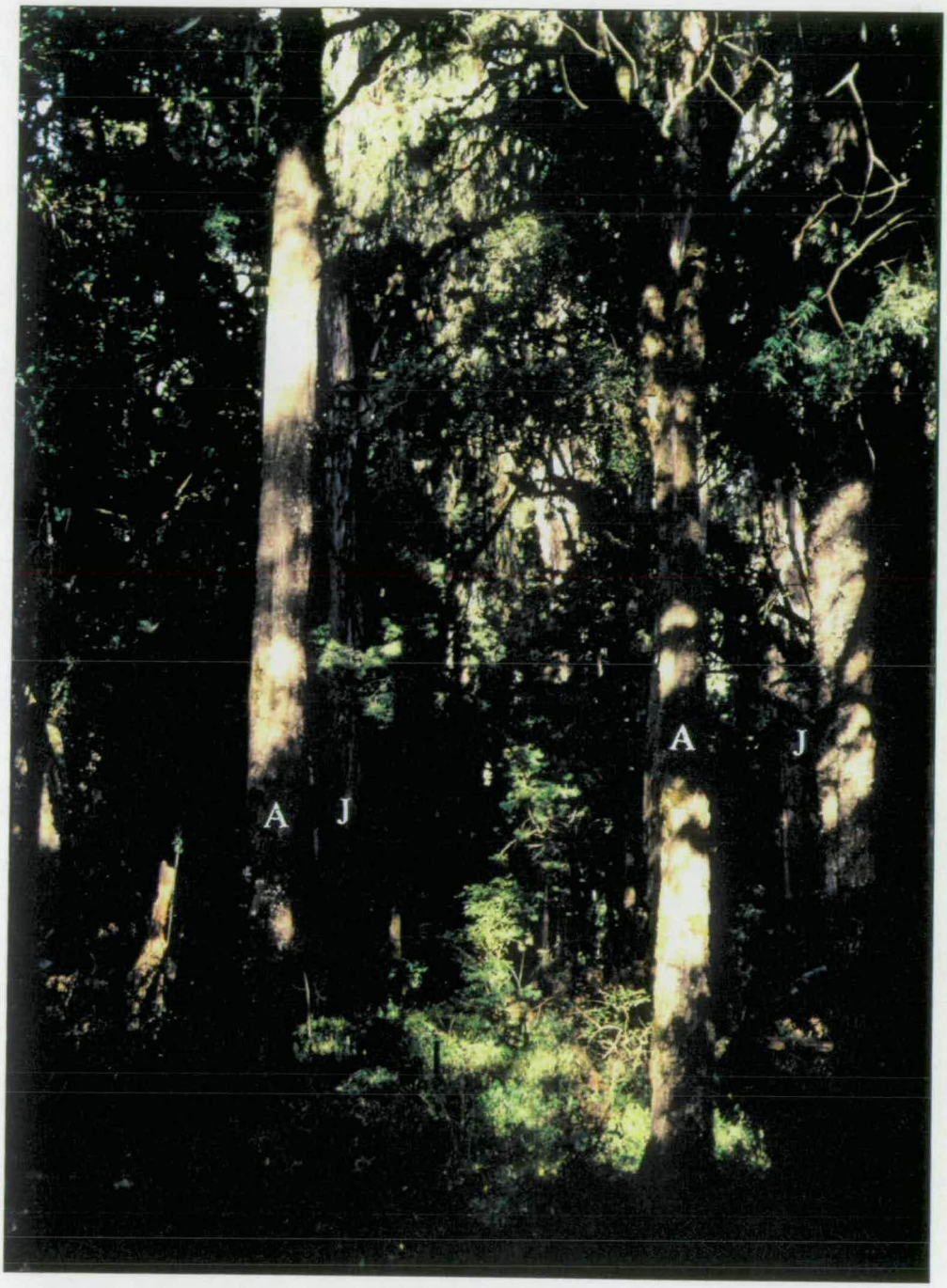

Figure 2.9: Photograph of *J. procera* and *A. gracilior* mixed forest stand in Arba-gugu forest, Ethiopia, at an altitude of 2500 m, showing the forest environment. *J. procrea* (*J*) and *A. gracilior* (*A*). Note *A. gracilior* is taking over *J. procrea*.

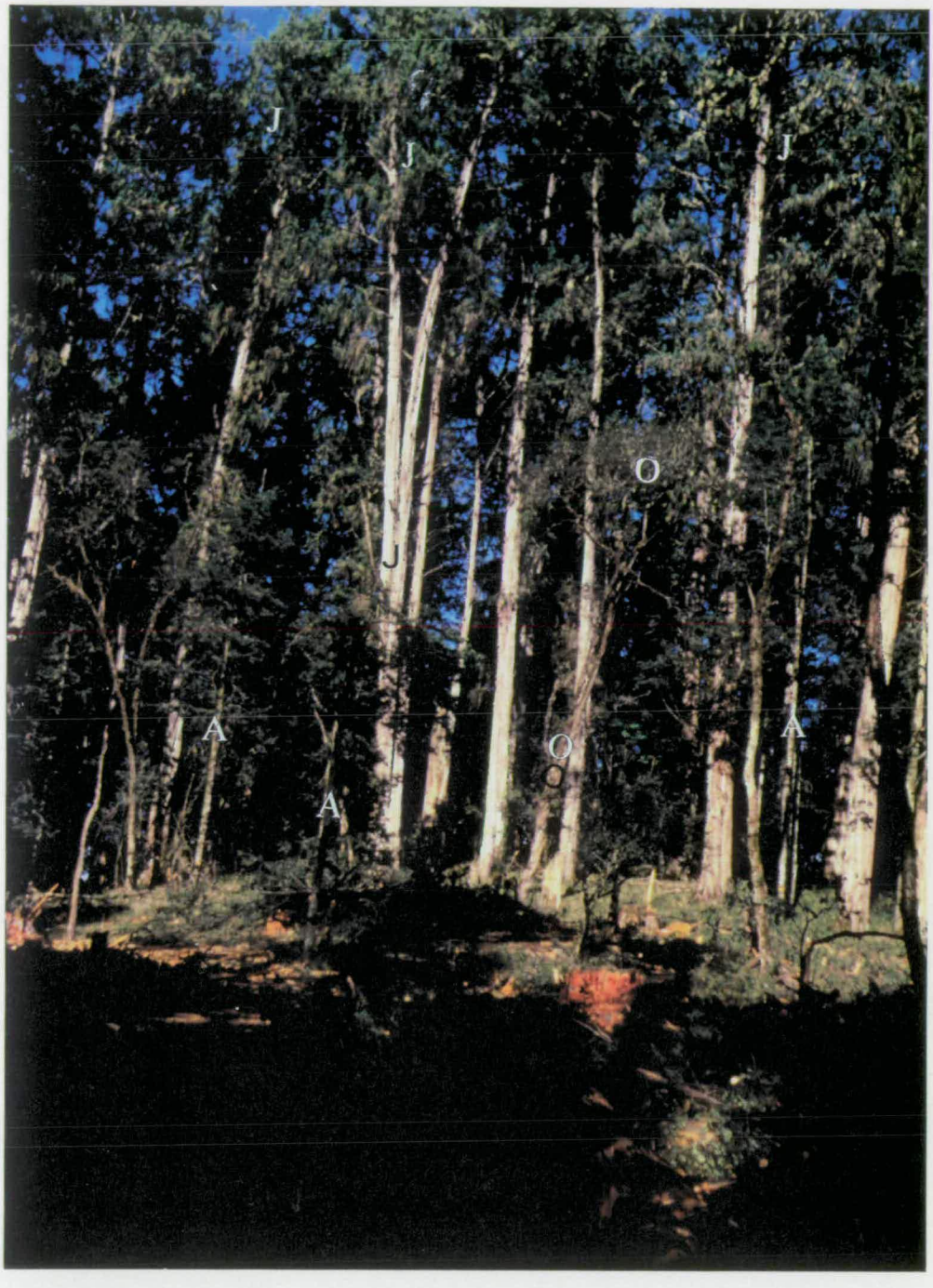

Figure 2.10: Photograph of *J. procera* forest stand in Arba-gugu forest, Ethiopia, at an altitude of 2700 m, showing the form of mature *J. procera* trees and the forest environment in relatively cooler and moist climate. *J. procera* (*J*), *Olea europea* ssp. *africana* (*O*) and *A. gracilior* (*A*). Note the density of mature trees and the young *A. gracilior* trees under the canopy trees ready to replace *J. procera*.

Table 2.2: The main characteristic tree species associated with *J. procera* and *Afrocarpus gracilior* in the Afromontane forests (AMFs). Source: Chaffey (1979) and White (1983).

	Species	Family
i.	**On most favourable sites**	
a)	**Upper storey:**	
	Afrocarpus gracilior (Pilger) C. N. Page	Podocarpaceae
	Allophylus abyssinica (Hochst.) Radlk.	Sapindaceae
	Apodytes dimidiata E. Meyer Ex Arn.	Icacinaceae
	Bersama abyssinica Fres.	Melianthaceae
	Chrysophyllum viridifolium Wood & Franks	Sapotaceae
	Juniperus procera Hochst. ex Endl.	Cupressaceae
	Hypericum revolutum Vahl	Guttiferae
	Ilex miti (L.) Radlk.	Aquifoliaceae
	Nuxia congesta R. Br. Ex Fresen	Loganiaceae
	Ocotea bullata (Burchell) Baillon	Lauraceae
	Pygeum africanum (Hook.f.) Kalkman	Rosaceae
	Rapanea melanophoeos (L.) Mez.	Myrsinaceae
	Schefflera abyssinica (Hochst. ex A. Rich.) Harms.	Araliaceae
	Olea europea L. *ssp. africana* Mill	Oleaceae
	Hagenia abyssinica (Bruce) J. F. Gmelin	Rosaceae
b)	**Lower storey:**	
	Carissa edulis (Forsk.) Vahl.	Apocynaceae
	Halleria lucida L.	Scrophulariaceae
	Myrsine africana L.	Myrsinaceae
ii.	**On lower altitude and drier sites**	
a)	**Upper storey:**	
	Olea europea L. *ssp. africana* Mill.	Oleaceae
	Acokanthera schimperi (A.DC.) Oliver	Apocynaceae
	Euphorbia candelabrum Trémaux ex Kotschy	Euphorbiaceae
b)	**Lower storey:**	
	Carissa edulis Vahl	Apocynaceae
	Dodonaea viscosa Jacq.	Sapindaceae
	Euclea schimperi (A.DC.) Dandy	Ebenaceae
	Maytenus undata (Thunb.) Blakelock	Celastraceae
	Rhus abyssinica Hochst. ex Oliv.	Anacardiaceae
	Vernonia amygdalina Del.	Asteraceae

Ethiopia, it can be found either as an accompanying tree with *J. procera* in the montane dry evergreen coniferous forests or as a dominant tree with broadleaved species.

A. gracilior in its mixed form with broadleaved forests in Ethiopia, dominates at mid-altitude and in sheltered valleys, and is associated with a great variety of hardwood species (Table 2.2). *A. gracilior* is the most frequent large species and with *Warburgia ugandensis* and *Syzygium guineense* emerges above the canopy and *J. procera* is absent from these forests. The two commercially important shrubs, *Coffea arabica* and *Rhamnus prinoides* (used for flavouring local beer) occur in the forest under-storey (Chaffey, 1979).

2.1.6 Silvicultural issues

i) Regeneration/Succession

a) *Juniperus procera*

J. procera is reputedly a strong light demander and does not regenerate under shade, and its seedlings are unable to penetrate a deep layer of humus on the surface of the soil (Gardner, 1926). Hence, its regeneration seems to be dependent on the disturbance of both the canopy and humus layer for a full exposure of light and exposed mineral soil. These conditions are created sometimes by fire, or by natural tree fall (Gardner, 1926, Wimbush, 1937; Chapman and White, 1970; Hall, 1984). Fig. 2.11 shows *J. procera* regeneration along road sides following exposure of mineral soil during construction of extraction road.

The occurrence of pure, closed *J. procera* stands in a mean annual rainfall of 1,000 to 1,250 mm reflects the establishment of *J. procera* following heavy disturbance, mainly by fire. Wimbush (1937) reports that, *J. procera* advance growth which escaped fire will outgrow the undergrowth and assume dominance when it reaches about 8 m height at about 20 years of age, reaching about 30 m or more (full height) at the age of 80 to 90 years. There is a belief that these stands remain healthy and dominant in the canopy for 200-300 years until ultimately the crown of the old trees starts to die back and allow more light into the forest floor. By this time, the late successional broadleaved species are favoured and replace the dying *J. procera* to dominate in the climax forest (Hall, 1984). In contrast to *J. procera,* these species regenerate under

deep shade. In areas where *J. procera* forests are completely destroyed by fire, associated species have become dominant colonisers (Greenway, 1955). The successful regeneration of *J. procera* is attributed to the occasional occurrence of fire damage. However, protecting *J. procera* from fire encourages the establishment of broad-leaved trees and encroachment of *J. procera* forests into grassland at the edges of the forest (Wimbush, 1937). This is probably why *A. gracilior* colonizes the *J. procera* forest stands (Fig. 2.9; 2.10).

In the northern parts of *J. procera*'s range in Africa and in Arabia with relatively low mean annual rainfall (<850 mm), the communities are more open and regeneration is related with the distribution of the parent tree. This makes successional relationships different to those in higher rainfall areas of *J. procera* forest. Under low rainfall the two important factors favouring regeneration are frequency of open ground within the vegetation, and the presence of steeply sloping land with little or no organic debris accumulation (Hall, 1984). However, increased frequency of fire in dry areas of eastern Africa are leading to replacement of *J. procera* by dense, fire-tolerant stands of other spp. (Frame, 1976, in Hall, 1984) and grazing of *J. procera* regeneration in Somalia, is ousting *J. procera* (Gilliland, 1952)

Moreover, the scarcity of viable seed of *J. procera* is also believed to have contributed to its decline. The well known unreliability of *J. procera* seed germination (e.g. Negussie *et al.*, 1991) in its natural range has been a constraint limiting the success of attempts to develop it as a major, widespread commercial species. To further worsen the situation *J. procera* cannot regenerate under natural conditions of closed canopy owing to the extreme shading, and its seeds cannot germinate on areas of thick humus surface (Gardner, 1926; Hall, 1984).

b) *Afrocarpus gracilior*

Various authors have given explanations for the lack of regeneration. Breitenbach (1963) blames browsing bush-buck, and thick mats of most-inflammable *Hypoestes* sp. and *Isoglossa* sp. preventing the roots of germinated *A. gracilior* seeds reaching the ground before the humid season ends in some Ethiopian forests. Lind and Morrison (1974) identify the twice-yearly inundation as the main cause in the Tanzania/Uganda border swamps forest. According to Chalk et al. (1935) once the serial stage in which *A. gracilior* grows vigorously commences, *A. gracilior* will inevitably grow steadily (up to 0.9 m $year^{-1}$). However, overall natural processes of

Figure 2.11: Photographs showing *J. procera* natural regeneration on disturbed sites, where mineral soil is exposed during road construction.

recovery are slow. A high representation of small to medium diameter classes of *A. gracilior* at Shashemene in Ethiopia (Breitenbach, 1963) has been attributed to unspecified events a few years earlier.

However, according to Chaffey (1979) *A. gracilior* and all other merchantable broadleaved species show a good diameter distribution and natural regeneration appears to be taking place in the undisturbed part of the forest. On the other hand, the diameter distribution of *J. procera* is with a high proportion of overmature trees and few specimens of younger trees. Table 2.3 presents an example of diameter (dbh) class distribution from a low-density inventory for *J. procera*, *A. gracilior* and all merchantable broadleaved species in Arba-gugu and Din-din forest together (Chaffey, 1979).

Table 2.3: Example of diameter size class distribution (stem number ha^{-1})of the two coniferous species and other merchantable broadleaved tree species for Araba-gugu and Din-din forest together. Source: Chaffey (1979).

	Diameter class cm									
Species	30	40	50	60	70	80	90	100	110	≥120
J. procera	1	1	1	1	2	1	1	2	1.3	2.6
A. gracilior	9	7	4	3	3	1	1	1	0.5	1.4
All broadleaved (merchantable)	7	6	5	3	2	1	1	1	0.2	0.2

For the stem numbers below 30 cm dbh, Ungethüm and Jordan (1990) for the same forest, estimate about 70-110 stems ha^{-1} of *A. gracilior* including saplings (as seen from Fig. 2.2 above). Also, high numbers of young *A. gracilior* trees, saplings and seedlings are to be found under *J. procera* stands (Fig. 2.10). Furthermore, *A. gracilior* natural regeneration is found in old logged sites (Fig. 2.12) except for the lack of management and protection. Both species produce seed freely and they have abundant seeds in the soil and on the forest floor. Yet, there are no signs of *J. procera* seedlings under similar conditions.

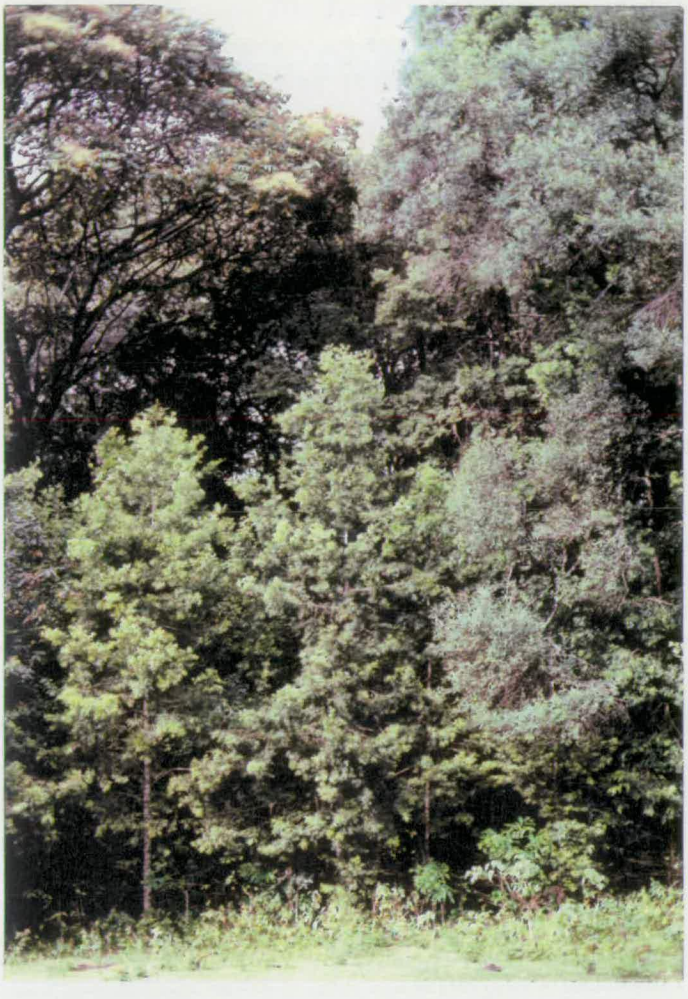

Figure 2.12: Example of *A. gracilior* natural regeneration (sapling stage) under *Hagenia abyssinica* (left) and *Olea europea* (right) foreground over an old logged and protected, but not managed site in Din-din forest.

ii) Defects and pests

There is some evidence of natural growth defects (Gardner, 1926) which indicates that the fluting and the resultant ingrowing bark have been caused by the persistence of the strong branches from top to bottom on the stem during the years of active growth of *J. procera* (Fig. 2.8). Trees with badly corrugated stems and ingrowing bark are not uncommon in natural *J. procera* forests. The problem of ingrowing bark can easily be avoided or at least reduced by growing *J. procera* in suitable localities under proper silvicultural management aimed at producing clean stems (Gardner, 1926).

The branches of *J. procera* trees are occasionally infested with a *Loranthus* parasite (Gardner, 1932). This is very similar to the host foliage making it difficult to observe. In some regions dwarf mistletoes cause a heavy loss every year.

2.1.7 Cultural and economic importance

i) *Juniperus procera*

a) Non-timber uses

In some parts of Ethiopia and Egypt *J. procera* has been considered as a sacred and holy tree (Vivi *et al.*, 1941; Jansen, 1981). In Ethiopia, churches are mostly constructed with *J. procera* poles and it is widely planted around churches for its shade, shelter, amenity and/or more importantly for its ritual values. The seedlings are planted around cemeteries and its branches and twigs are strewn on the corpse before filling the grave (Jansen, 1981). *J. procera* berries were used in Egypt as an embalming agent. According to Vivi *et al.* (1941) the berries have essential oil which has a special significance in anointing the dead body. The berries are also used in Egypt for fumigation.

Jansen (1981) reviews the medicinal value of *J. procera* reported from Ethiopia and elsewhere. These uses include the fruit as a sudoriferum, an emmenagogue (to stimulate menstrual flow), for curing skin diseases, against headaches (when mixed with other fruits); for the smoking of (fruiting) branches to relieve rheumatic pains; the twigs and buds against intestinal worms; leaves as a drench for horses and mules suffering from stomach disorders, against camel dermitis, active against

Mycobacterium tuberculoses, a podophyllotoxin (antibiotic) against tumours; powdered leaf to cure humans and animal wounds; the resin as a stimulant, against ulcers and when mixed with honey against liver diseases; the oil from the wood to induce abortion.

J. procera berries are best known for their high oil content. The oil in addition to its medicinal value, is best known for flavouring gin. The wood contains 2-3 % oil (known as cedar oil or cedar wood oil). This essential oil is obtained by distillation from wood and leaves. It has also been distilled from the sawdust (FAO, 1986). The most important component of the oil is Cedrol (23-76 %) which has a special importance in microscopy, soap, perfume/cosmetic and occasionally in the pharmaceutical industry. The bark contains about 3.5 % of tannin (Jansen, 1981).

J. procera is ecologically important in the Afromontane vegetation. As an evergreen species it is valuable for soil and watershed protection especially in rugged and mountainous terrain particularly at the beginning of the rain season. The species is considered to be one of the best candidates not only for soil conservation but also for reafforesting skeletal, nutrient deficient, dry and exposed hilly sites (Jones, 1989). In Ethiopia it represents one of the few indigenous candidates for rehabilitation and protection planting programmes.

The compact columnar or conical forms of *J. procera* are excellent for narrow avenues in gardens, hence it has good aesthetic value. The spreading variety of *J. procera* make a good ground cover in semi-arid places, while those of a bushy nature may be used for hedges. It is browsed by sheep and its berries attract birds. Healthy vigorous stands could, therefore, serve as valuable game viewing sites (Hall and Ndosi, 1982). The tree has an appreciable indirect potential to attract tourists and subsequently to augment national income.

b) Wood and timber uses

It has been found (Battiscombe, 1936) that *J. procera* wood has two distinctive properties: durability and extreme immunity against termite attack. The timber is durable against rotting both above and below ground under all conditions and is entirely resistant to attack by borers. This extreme resistance to termites and rotting fungi is attributed to its oleo-resin content.

J. procera wood is fine-textured and straight grained with growth zones not plainly marked and of little to medium hardness/strength. The wood is extremely fissile, brittle at the edges and prone to split during nailing. The heart-wood is very durable, whittles well and works easily. It takes polish well, is very fragrant and glues well. *J. procera* wood is resistant to impregnation with oils and hence only thin materials can be satisfactorily impregnated (Dale and Greenway, 1961).

In east Africa *J. procera* is mainly viewed as a timber tree. Despite its tendency to split when nailed it has been used extensively for construction that needs or does not need nailing. In Kenya, as well as in Ethiopia, no other tree species is more widely used for house construction, roofing-shingles, beams, floor boards, fence-posts, plant trays, water flumes, doors, windows, panelling, furniture and telegraph poles (Battiscombe, 1936; Dale and Greenway, 1961; Kigomo, 1985). Likewise, it has a considerable potential in chipboard production and may be used in the manufacture of hardboards and particle-boards (FAO, 1986).

The use of *J. procera* wood in pencil production is gaining considerable significance. Following the gradual decline in supplies of American pencil cedar (*Juniperus virginiana* and *J. bermudiana*) a number of non-cedar species have been tried and used as a substitute. *J. procera* produces timber with all the desirable qualities: red colour, distinctive fragrance of the pencil cedar and durability combined with ease of sharpening (FAO, 1986).

ii) *Afrocarpus gracilior*

a) Non-timber uses

Cambe *et al.* (1984) identified 12 phenolic diterpenoids from 10 species of Podocarpaceae including *A. gracilior*. Kubo *et al.* (1983, 1984) isolated chemical compounds with insecticidal potential from the leaves. Oil extracted from the seeds or fruits is used as medicine to treat gonorrhoea (Breitenbach, 1963) and as edible oil (personal observation, 1991). It is widely acknowledged that the tree is very suitable for planting along road sides in cities because of its excellent and attractive form.

b) Wood and timber uses

A. gracilior furnishes an excellent timber of an attractive yellowish-brown colour with no distinction between sapwood and heartwood. The wood is generally straight grained, very fine and featureless. It is non-resinous and lacks scent and taste (Bryce, 1967). It is soft to moderately hard and medium density. The timber saws easily and works well with all tools. It glues well and takes paints and varnishes satisfactorily. The timber dries fairly rapidly, with some splitting and a strong tendency to distort (Bryce, 1967). The distortion is caused by abnormal longitudinal shrinkage due to spiral thickening in tracheid walls (Brown, 1957) and sometimes to the presence of the compression wood (Bryce, 1967). For this reason its timber is classified as timber with small movement (Bryce, 1967). The timber is susceptible to pin-hole borers, blue-stain fungus (freshly sawn timber), powder-post beetle attacks and decay (Bryce, 1967). Research findings indicate that untreated *A. gracilior* timber decays in the ground within 3-5 years (Breitenbach, 1963). The wood is easy to treat with preservatives (Dale and Greenway, 1961).

The timber of this species is a standard building timber in most of east Africa and is widely used for floor joists and roofing, though not suitable for external joinery or door frames. It is also used in furniture, boxes, crates, shelving, drawer linings, shop counters and light duty impregnated railway sleepers (Bryce, 1967). From Tanzania, Kenya and Uganda, large quantities of sawnwood were exported to South Africa and Europe in the past (Bryce, 1967). In Ethiopia, about 60 % of the total sawn timber in the country used to come from *A. gracilior* (Breitenbach, 1963). Even today, where the species is reduced to only few inaccessible areas, it is the preferred timber species in Ethiopia, when found in a logging area.

2.2 Description of the forest study area

2.2.1 Location of the study site

To identify, select and locate the field study site, an examination of aerial photographs and maps of the Afromontane coniferous forests of Ethiopia was made, and a reconnaissance survey was conducted of seven forests (Adaba-Dodola and Sanete-Batu in Bale, Negele and Arero in Borena, Menagesha in Shoa, Din-din in Harerghe and Arba-gugu in Arsi regions). The Arba-gugu forest was selected. The

forest is located on the southern escarpment of the Rift Valley about 200 km south east of Addis Ababa at about 39° 45' to 40° 10' E and 8° 15' to 8° 35' N (Fig. 2.13). This forest extends further to the north-east to the forest of Din-din.

2.2.2 Physiography and drainage

The topography is rugged and characterized by a chain of mountains orientated roughly ENE-WSW and deeply cut valleys with about 70% of the area exceeding 30° slope (Ungethüm and Jordan, 1990). The smaller ridges and foothills adjoining the main ridge are steep and sharp. Towards the western extremity, the ridge becomes less distinct and the slopes more moderate. The altitude ranges from 2100 m to more than 3300 m above sea level. The mountain ridge drains into the tributaries of the Awash river in the Rift Valley in the north and into the Shelele in the south by means of few permanent streams and seasonal water courses.

2.2.3 Geology and soils

The parent material is of volcanic origin similar in type to that of most of the Ethiopian highlands. Rocks are mainly alkaline basalt and tuffs with rare rhyolites (Kazmin, 1975). The soils are well drained, varying from black to brown or reddish brown, well structured and of medium texture. The soils in valleys and depressions and on gentle slopes are deep. Soils are generally shallow and stony on the steeper slopes and on ridge tops with numerous exposures of rock outcrops.

2.2.4 Climate

The climatic pattern is typical of that of the central parts of the Ethiopian Plateau (Chaffey, 1979). The bimodal rainfall distribution has one main wet season from June to September usually preceded by a less pronounced short rainy period during March and April. However, there is no month without precipitation. The mean annual rainfall at Guna meteorological station, located at an altitude of 2600 m in the immediate vicinity of the study area, varies from 850 mm to 1200 mm with about 115 rainy days. The mean annual rainfall for 1989 and 1990, obtained from Guna and Aseko (2100 m altitude) meteorological stations about 15 and 10 km to the west and east of the study site, was 1186 mm. The rainfall during March and April accounted for 9% and 17% respectively of the mean rainfall for the same period (1989 and 1990) (see Appendix 2.1). The coldest time of the year was also the driest while maximum temperatures

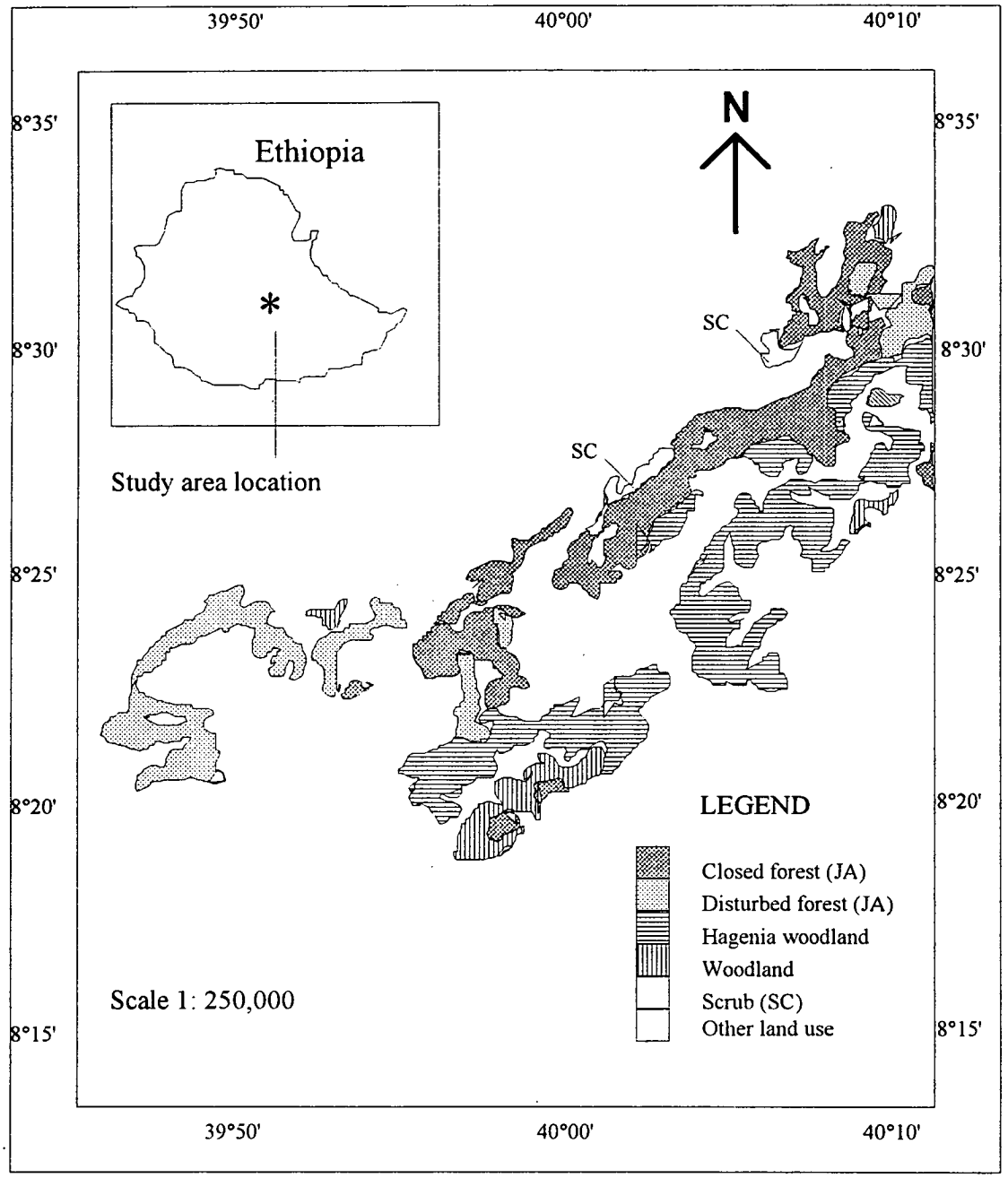

Figure 2.13: Map showing the location of the study area, and the distribution of the Arba-gugu forest vegetation.

occurred before the onset of the main rain. The monthly temperature ranged from 7.5 °C mean minimum to 25 °C. Winds are mostly from the north east and south east, the main wet season being associated with the convergence of the two air streams (Chaffey, 1979).

2.2.5 The forest vegetation

This forest has been described by Breitenbach (1963) and Chaffey (1979). The two coniferous species dominate the altitude between 2100 and 2800 m, while *Hagenia abyssinica* woodland dominates above this point. Although some stands are found on relatively gentle slopes, most of the remaining forest occupies a steep and dissected ridge. The forest is composed primarily of *Juniperus procera* and *Afrocarpus gracilior* forming a fairly open canopy with the height reaching 40-45 m and a diameter at breast height of up to 2 m. Table 2.4 provides the list of the main tree, shrub and grass species associated with *Juniperus procera*, based on the description given by Breitenbach (1963), Kelecha (1977) and Chaffey (1979). Except for *Panicum monticolum* Hook. F., the ground flora is generally poor and maintained by grazing pressure. The forest floor is covered mainly with thick unbroken litter of the two coniferous species.

Ungethüm and Jordan (1990) estimated the total forest area to be more than 29000 hectares including Din-din of which only about 8500 ha is estimated to be closed forest. They also stated that the coniferous forests encountered in Arba-gugu constitute an extremely rare forest type in Africa, and recommend thorough protection due to their limited natural extension of only a few thousand hectares.

The total standing volume was estimated to be 400-450 m^3 ha^{-1} depending on the successional stage of the forest (Ungethüm and Jordan, 1990). However, standing volume for all timber species >30 cm dbh was given as 190 m^3 ha^{-1} (Chaffey, 1979). Of the estimated 95 m^3 ha^{-1} merchantable timber, about 89% was of the two conifers.

The forest has been heavily exploited by up to 5 sawmills since 1960, but now only one sawmill due to the shortage of logging material. The felling system is not based on the specific regeneration requirement of the forest, and is not different in this forest to that described in Section 2.1.4 above.

Wild animals such as Menelik's bush buck, Nyalla antelope and black winged love bird (*Agapovnis taranta*), and others such as warthog, wild pigs, civet cat, colobus monkey, baboons and various apes found in this forest (Ungethüm and Jordan, 1990) are also endangered due to the fast disappearance of the forest.

Table 2.4: List of main tree, shrub and grass species associated with *Juniperus procera* in Arba-gugu forest. Source: Chaffey (1979).

	Species	Family
i.	**Tree species:**	
	Afrocarpus gracilior (Thunberg) R. Brown	Podocarpaceae
	Croton machrostachyus Hochst. ex. A. Rich	Euphorbiaceae
	Ekbergia capensis Sparrman	Meliaceae
	Ficus spp	Moraceae
	Juniperus procera Hochst. ex. Endl.	Cupressaceae
	Hagenia abyssinica (Bruce) J. F. Gmelin	Rosaceae
	Hypericum revolutum Vahl.	Hypericaceae
	Olea europea L. ssp. *africana* Mill.	Oleaceae
	Olea hochestetteri Bak.	Oleaceae
	Pygeum africanum (Hook.f.) Kalkman syn. *Prunus africanum*	Rosaceae
	Syzygium guineense (Willd.) DC. ssp. *afromontanum* F.White	Myrtaceae
	Teclea noblis Del.	Rutaceae
ii.	**Shrub species**	
	Bersama abyssinica Fres.	Melianthaceae
	Brucea antidysenterica J. F. Mill.	Simaroubaceae
	Carissa edulis (Forsk.) Vahl.	Apocynaceae
	Cassipourea malosana ((Bak.) Alston.	Rhizophoraceae
	Dodonea viscosa (L.) Jacq.	Sapindaceae
	Dovyalis abyssinica (A.Rich) Warburg.	Flacourtiaceae
	Erica arborea L.	Ericaceae
	Maytenus ovatus Var. ovatus. (Hochst.) Loes.	Celastraceae
	Myrsine africana L.	Myrsinaceae
	Osyris compressa (Berg.) A. DC.	Santalaceae
	Rhus spp	Anacardiaceae
	Rubus spp	Rosaceae
	Sideroxylon oxyacantha Baill.	Sapotaceae
	Vangueria edulis Vahl.	Rubiaceae
iii.	**Grass species:**	
	Panicum monticolum Hook. F.	Poaceae

2.6 Population and forest land use

It is estimated that population density in and around the forest is about 100 per km^2 (Ungethüm and Jordan, 1990). The population living in the area covered by this study is an agricultural community. Generally, the relationship between the local people and the forest and the land use is similar to other forests and described in Section 2.1.4 above. They depend mainly on livestock, sheep and traditional bee keeping. Recently, however, they have started farming and growing wheat, barley and maize as the principal crops. The forestry activities provide fresh agricultural land for the community.

CHAPTER 3

Light and Temperature Regimes in the Understorey of an Afromontane Coniferous Forest

3.1 Introduction

The success of dominated trees, understorey species and seedlings depends on their ability to utilize the attenuated radiation that reaches the lower strata of the canopy (Chazdon, 1988). There is a strong spatial variability of solar radiation in forest understorey, which determines the distribution of understorey vegetation (e.g. Pearcy 1983, Chazdon and Fetcher 1984).

Understorey trees may be exposed to light of quite different quality to the overstorey trees. Radiation that passes through the canopy is altered in its spectral composition (Holmes and Smith, 1977). Crowns of the overstorey absorb part of the blue and red light and reflect or transmit green, yellow and far-red. Hence, the understorey light environment is characterized by a low ratio of red (655-665 nm) to far-red (725-735 nm) radiation (R/FR ratio) (Smith, 1981). Canopy rearrangements caused by gap formation may also bring significant changes in the light environment of understorey plants which may trigger germination of seeds or the onset of growth of seedlings and saplings (see references cited in Denslow, 1987 *et al.*; Canham, 1989).

Open sites may become hot and dry, in contrast to the shaded microclimate of the forest floor. During the day, the leaves in the canopy intercept most of the solar radiation, so that leaf and air temperatures at the forest floor are moderated. There are many other influences of the canopy on the microclimate. The canopy prevents rapid loss of heat from the trunk area through radiation to space at night, making the air temperature higher than outside the forest (Wenger, 1984). Temperature directly affects the day-to-day physiological processes of plants and indirectly influences their seasonal cycle of development (Fowells and Means, 1990). Plants vary greatly in their

photosynthetic response to temperature, depending upon the kind of conditions they experience in their natural environments.

Soil moisture is one of the most important factors for the germination and establishment of understorey vegetation (Harper *et al.*, 1965), and information on soil moisture content of a forest will be essential.

Considerable interest has surrounded the characterization of light environments of tropical rainforests (e.g. Pearcy 1983; Chazdon and Fetcher, 1984; Chazdon 1986; Lee, 1989). The light environment of temperate deciduous forests has also been characterized (e.g. Anderson, 1964a; Reifsnyder *et al.*, 1971; Hutchison and Matt, 1976; Weber *et al.*, 1985). Other workers have also reported the light environment in the temperate coniferous forests (Reifsnyder *et al.*, 1971; Young and Smith, 1979, 1983; Salminen *et al.*, 1983; Vales and Bunnell, 1988; Ustin *et al.*, 1984; Canham *et al.*, 1990). In contrast, there appear to be no published reports of dedicated measurements of variation in either light quantity or quality, or air temperature in the Afromontane *Juniperus-Afrocarpus* coniferous forests.

Complete and exact quantification of a forest environment is practically impossible. Three environmental factors are of particular importance in influencing the germination of tree seeds and the performance of seedlings (see review by White, 1983; Vázquez-Yanes and Orozco-Segovia, 1984). Therefore, the primary goal of this study is to understand the variation in radiation, air temperature and soil moisture of the *J. procera* and *A. gracilior* forest in Arba-gugu. The specific objectives of this study include the following:

1. to characterise the spatial and temporal variability of photosynthetic photon flux (PPF) and Red:Far-red ratio (R:F-r).

2. to characterise the proportion of direct and diffuse radiation and the 'sunfleck environment' of the forest understorey.

3. to characterise the understorey air temperature in relation to the radiation input in the open.

4. to investigate the soil moisture contents in the understorey and at an open site and find its relationship with radiation and/or air temperature.

5. to develop an empirical model for estimating percentage light transmission in the forest understorey using values from sensor measurements and photographic estimation.

3.2 Material and methods

3.2.1 Site selection

One site representing a range of light environments in the Arba-gugu forest was selected for detailed measurements of photosynthetic photon flux (PPF), air temperature, soil moisture and canopy cover. The site was located on a north-west facing slope of about 20° at altitude of 2520 m at Sengo-kone. It extends towards a hill on its south-eastern limit. Within this site nine locations were selected for the measurements: a large clearing of about 1 ha and eight locations covering a range of canopy densities (gap edge, closed, medium and open canopy) (Fig. 3.1).

The large clearing was about one year old and approximately rectangular, oriented north-east to south-west. In its south-west direction all the trees were cut except for very few scattered and lopped individuals. It measured about 60 m east-west and about 170 m north-south. The large clearing was obstructed from direct sunshine in the early mornings (up to 8:30 am) and late afternoon (beginning 3:30 pm) due to the shade from uncut trees. This large clearing will be referred hereafter as open. The eight locations in the understorey measured approximately 45, 53, 62, 65, 68, 70, 71 and 75 metres east, west and north-west of the centre of the open site. This permitted the simultaneous measurement of PPF and air temperature in the open and one location in the understorey. Sensors were placed in the open and understorey locations. Vertical photographs of the canopy were taken at each location to estimate the canopy cover and explore the relation between gap fraction and PPF.

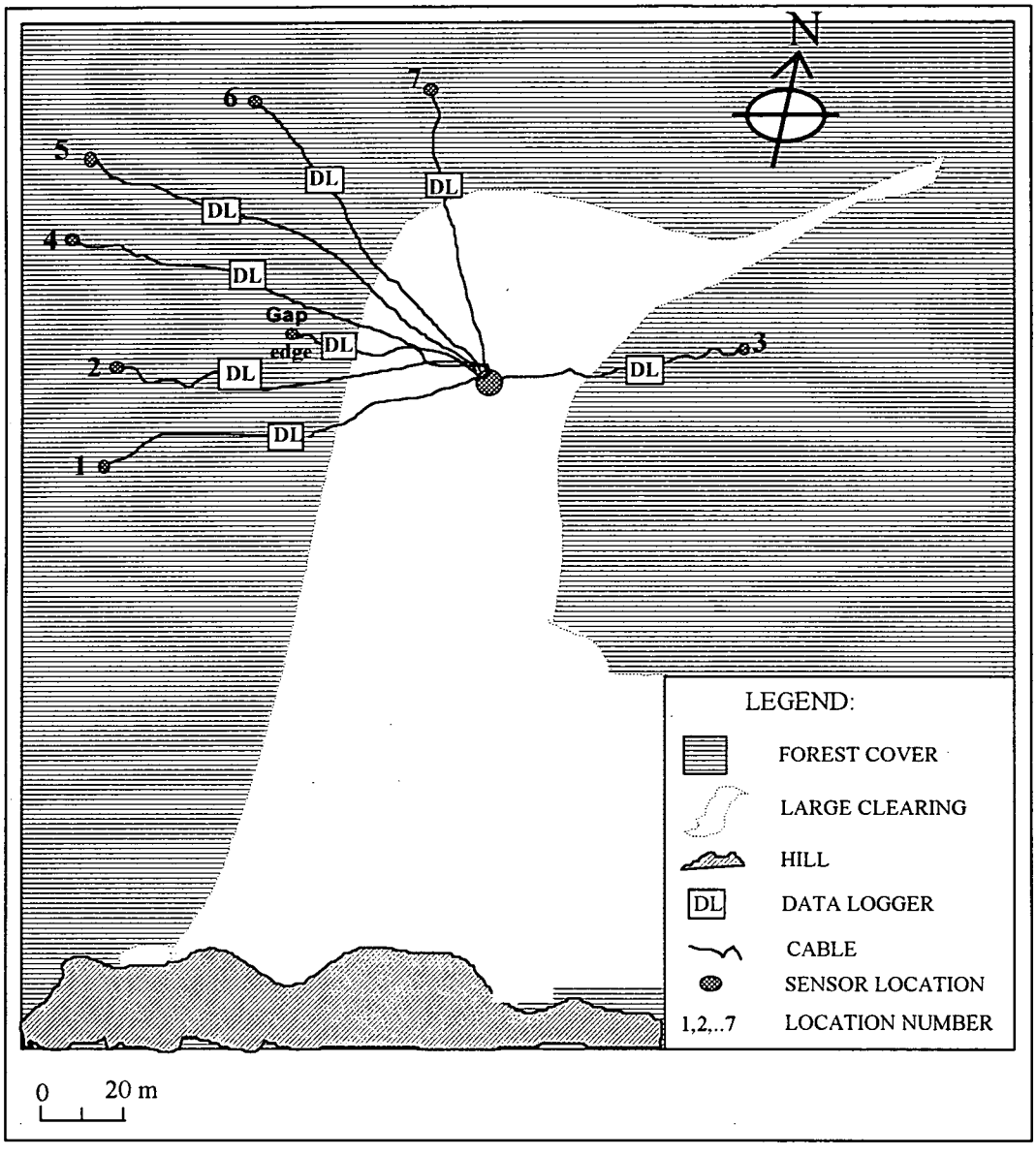

Figure 3.1: Sketch map showing locations of environmental measuring instruments in *J. procera* and *A. gracilior* forest understorey and large clearing (open) site at Sengo-kone, Arba-gugu forest.

3.2.2 Light measurements

i) Photosynthetic photon flux (PPF) measurements

Two quantum sensors were used to measure the penetration of photosynthetic photon flux (PPF) into the canopy. The sensors were calibrated against a standard quantum sensor (Li-190SB Li-Cor., Lincoln, USA) on a clear sunny day. The standard sensor was new, calibrated by Li-Cor, and supplied with a calibration certificate. The two sensors were connected to a battery powered data logger CR21, (Campbell Scientific Inc. Loughborough, UK) using 50 m cables on each. One sensor was permanently located in the open, and the second sensor was located at one of eight different locations arbitrarily chosen to represent a range of canopy densities. Both sensors were mounted rigidly and horizontally on posts at 60 cm above the ground. Measurements were taken every 5 minutes and stored as 1-hour averages on the data logger for local standard time. The daily PPF data were dumped every 2 days both to a Toshiba T1000 laptop computer, and a magnetic tape recorder. The sensor located in the open recorded PPF more or less continuously for 26 days between 17th March and 22nd April 1991. Due to the limited number of channels and storage locations in the data logger it was not possible to duplicate the measurements at the eight locations. Thus, the second sensor was moved between the eight locations every 3-4 days.

The weather conditions varied irregularly throughout the sampling period with alternately clear and cloudy (or rainy) periods. Since one sensor permanently monitored the open (macroclimate), data from sensors inside the forest (microclimate), can be discussed in terms of relative values, whatever the weather conditions.

(ii)Estimation of light from hemispherical photographs.

a) Canopy photography

Because of the large number of light sensors that are needed to obtain reliable estimates of PPD over the spatially very variable forest, alternative approaches have

been developed, based on measurement of canopy structure and the use of an empirical model to predict the spatial distribution of irradiance (Kuuluvainen and Pukkala, 1987; Pukkala *et al.*, 1991). Hemispherical photographs taken from the forest floor can potentially provide valuable estimation of the direct and diffuse radiation environments beneath forest canopies over a scale that would not be economical using light sensors attached to data loggers (e.g. Evans and Coombe, 1959; Anderson, 1964; Salminen *et al.*, 1983; Canham *et al.*, 1990).

Hemispherical (fisheye) photographs of the forest canopy were taken at the nine sensor locations with a Nikon camera fitted with a Nikon 7.5 mm f5.6 Fish eye lens (produced by Nippon Kogaku, Japan). The camera was mounted on a tripod with the lens pointing to the zenith. It was levelled with a bubble level mounted on the body of the camera to ensure that the film plane was horizontal. The camera was orientated such that Magnetic North was always located at the top of the photographs, facilitating overlay of the solar track during the analysis. Exposures were based on the light values of the open sky at the open site using a Weston Mark IV exposure meter. This ensured standard brightness of the sky in the resulting image, with effectively under exposed foliage to enhance the contrast between foliage and sky. A long pneumatic cable release was used to avoid the inclusion of the operator in the picture. Black and white technical pan film (Kodak) was used with film speed ISO 100. In order to characterise the canopy cover at seedling height and the effects on the understorey radiation environment, the photographs were taken at 60 cm above ground. All photographs were taken in windless conditions with overcast sky within an hour of sunrise or sunset to ensure even backlighting.

Development was adjusted to obtain low contrast. The solution was prepared by dissolving 10 g of sodium sulphite and 0.5 g of phenidone (1-pheny-3 pyrazolidene) in 150 ml dionised water at 35 °C and diluted to 330 ml with cold water. The films were developed for 17 minutes at 20 °C with 30 seconds of initial agitation and two inversions every 30 second thereafter. Soft-tone photographic paper was used to avoid elimination of bright leaves in the printing process. The films were printed on 19 x 24 cm paper giving a circular image of 18 cm diameter.

b) Analysis of hemispherical photographs

1) Estimation of gap frequency and diffuse radiation

Photographs were analyzed using the grid analysis procedure prescribed by Anderson (1964) to estimate gap frequency and percentage transmission (Fig. 3.2a). A transparent 'spider's web' overlay 18 cm in diameter was constructed to fit the size of the hemispherical photographs. The spider's web had 20 concentric annuli, each annulus containing an equal area of sky dissected with 50 radial lines spaced to give cells representing equal areas of sky, producing a grid of 1000 segments constructed using a computer program written by Legg (1993). The transparent spider's web was placed over the hemispherical photographs and analysed to estimate the percentage shade (canopy cover) or open sky (gap fraction) and percentage transmission. The segments were classified into four categories, viz., 100, 75, 25 and 0 % of open sky. The scoring was done annulus by annulus. From these scores gap frequency and total percentage transmission of diffuse light through the canopy was calculated.

2) Direct radiation

The direct radiation at a site is determined by the elevation of the sun, the obstruction of the sun's rays by neighbouring trees, hills or other objects, and the slope and aspect of the ground itself. Following Evans and Coombe (1959), solar tracks were used to measure the proportion of sun's path unobstructed by a forest canopy for subsequent calculation of insolation properties of the site at latitude 8° 20' N.

A computer program written by Legg, 1993 (unpublished) was used to construct a solar track diagram and calculate both direct and diffuse radiation based on equations provided by Page and Lebens (1986) and Pearcy (1989).

The predicted radiation estimated photographically for local time (Fig. 3.2b) and the PPF measured using quantum sensors were compared for different dates of the period of field study (March/April, 1991).

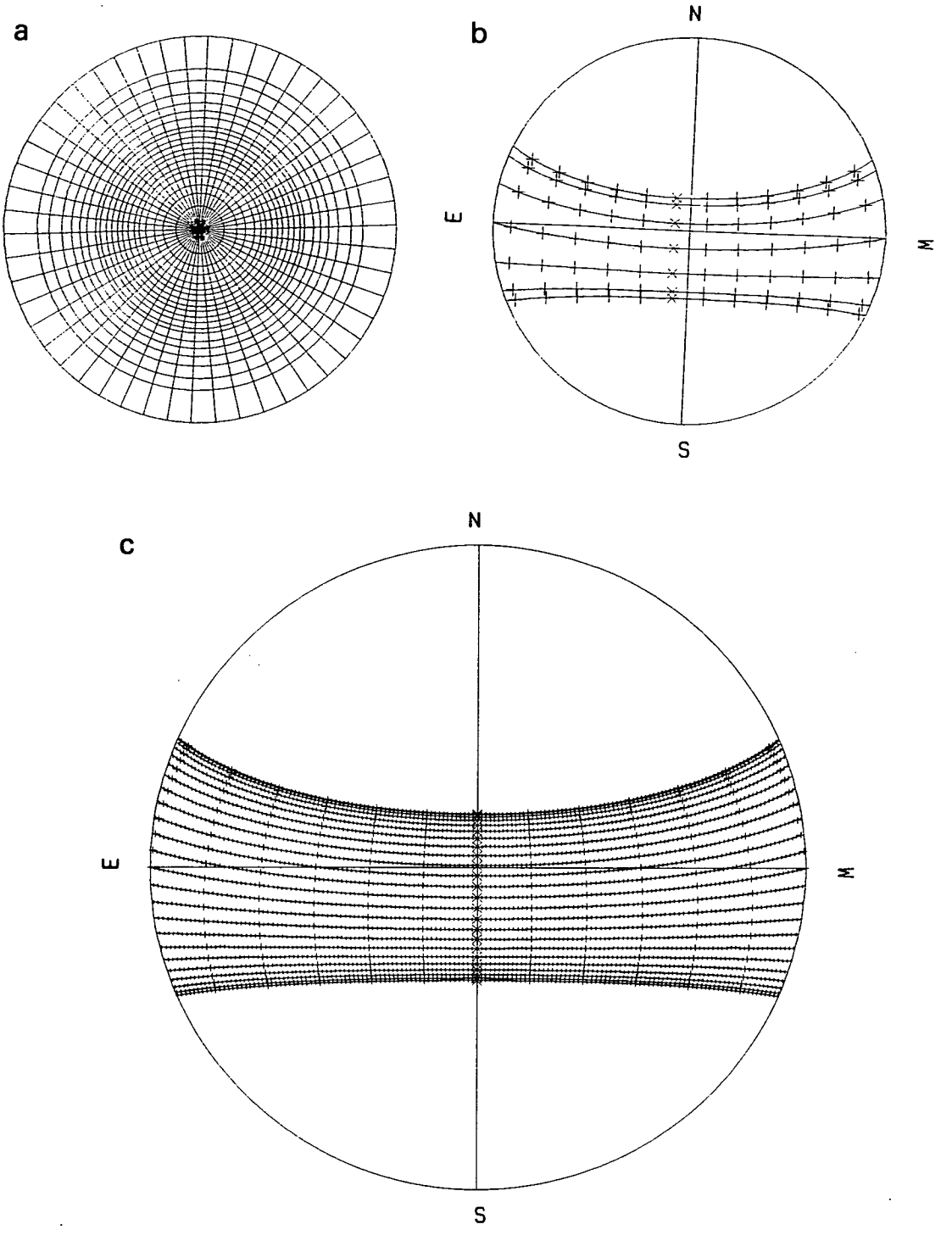

Figure 3.2: a) Diagram of spider's web grid; solar tracks calculated for 8° 20'N latitude and 40° 0'E longitude calculated for b) local time on the 21st of each month December to June, and c) every quarter-month for solar time.

For studies through the year a transparent overlay based on solar time for 25 solar tracks at quarter-month intervals and at 5-min intervals for each day from 21st December to 21st June was constructed to read the sunshine hours for each of the solar tracks representing 50 days in the year (Fig. 3.2c). Transparent overlays produced from the solar track diagrams were superimposed on the hemispherical photographs orientating to the True North after making correction for magnetic declination. An open point along a track was considered as potential sunshine. For this evaluation, it is assumed that 100% of the potential direct PPF penetrates through every canopy opening and that none penetrates through a closed point. Direct Site Factor was defined as the proportion of sky directly visible along the path of the sun during the period 21st December to 21st June.

Direct and diffuse site factors refer respectively to photographic estimations of the proportion of direct and diffuse radiation levels under a canopy relative to the level outside (above) the canopy (Anderson, 1964).

(iii) Red:Far-red ratio measurements

A red:far-red ratio sensor (SKR 110, Skye Instruments Ltd., Powys, Wales, UK) was used to measure R:F-r ratio, defined as photon fluence rate centred at 660 and 730 nm respectively. The sensor was connected to the delta logger (Delta-T Devices Ltd, Cambridge, UK). The red and far-red photon fluence rate was monitored on separate channels for 6 days in the open and in the understorey (open canopy, medium canopy and closed canopy densities for 2 days in each) during December 1992. Sensors were monitored at 5-seconds intervals and the data logger recorded 30-min averages.

3.2.3 Air temperature measurements

Air temperature measurements were made using thermistor probes calibrated in a controlled-temperature water bath. In use, the thermistor probes were protected from direct solar radiation with a radiation shield constructed using aluminium covered with melinex. Two sets of thermistor probes were connected to the data logger using 50 m

cables and located side by side with the quantum sensors at the locations described in 3.2.1 above. Data recording and collection were as described for PPF measurements.

3.2.4 Soil moisture contents

The state of water in the soil was described in terms of the quantity present using gravimetric analysis following the method described by Gardner (1986) (in Rundel and Jarrell, 1989). At each location (both in the large clearing and eight understorey locations) the soil over an area of 50 cm x 50 cm was excavated to a depth of 30 cm, brought together, mixed thoroughly and aggregated into one unit to form a compound sample and returned to the pits to equilibrate with the soil environment for a week before taking samples. One hundred grams of fresh soil was taken and weighed every 7 days from each location using a Mettler PM 6000 balance. The fresh soil sample was air dried and kept in a plastic bag until it could be oven dried. The soil sample was dried for one hour at 130 °C to constant weight using a Heraeus oven in the Forestry Research Centre laboratory in Addis Ababa.

3.3 Data analysis

3.3.1 Light data

Daily regimes of observed PPF of the open and understorey locations for the period between March 17 and April 22, 1991, were calculated. Mean daily total PPF, daily average and range for the eight understorey locations were calculated using 3 to 4 days data for each location and for relevant days in the open location. Unfortunately, at the open site there was obstruction of the sun in early morning and late afternoon. Therefore, the percentage PPF transmissions in the understorey were calculated over 6 hours (9:00 to 15:00) to give total PPF data centred at noon in the understorey relative to the open. Also PPF transmission on high and low PPF days for each location were calculated over 6 hours only (9:00 to 15:00).

Daily mean and range of Red:Far-red ratios and PPF for the same period in the open and in the understorey locations (open canopy, medium canopy and closed canopy densities) were calculated.

For each photograph, hourly and daily instantaneous direct, diffuse and global (direct + diffuse) radiation was calculated for latitude 8° 20' N, longitude 4° E and altitude 2520 m based on equations given by Gates (1980) and Page and Lebens (1986) using a computer programme written by Legg (1993). The proportion of direct and diffuse PPF transmitted at the open and understorey locations were computed using calculated radiation, percentage canopy cover (gap fraction) and sunshine hours estimated from hemispherical photographs for days on which light was measured at the same location. This could be compared with percentage transmission of PPF through the forest canopies obtained from the quantum sensors. For each location, number of minutes of sunflecks per day, diffuse PPF as a percentage of global radiation and percent contribution of sunflecks for measured daily PPF was calculated. For each photograph, yearly and monthly potential numbers of minutes of sunflecks per day, sunfleck duration and the direct site factor were calculated for each location, from 25 solar tracks representing the quarter months between December 21st and June 21st. The proportions of diffuse and direct PPF to global PPF were estimated.

An empirical model linking measured PPF to gap-fraction (percentage canopy cover) was developed using percent open PPF data of all locations obtained from quantum sensors and percentage canopy gap (gap fraction) of all locations estimated from hemispherical photographs

3.3.2 Air temperatures data

Mean diurnal cycles of air temperature in the open and in the understorey were calculated for the period between March 17 and April 22, 1991. Mean diurnal patterns of PPF of the understorey were calculated as hourly means from 3 to 4 days observation at each location, with corresponding data from the open site. The air temperature differences between the open and understorey, and differences between day and night were calculated.

3.4 Results

3.4.1 The light environment

(i) Photosynthetic photon flux (PPF) sensor results

Total daily photosynthetic photon fluxes (PPF) in the open, edge-of-gap and seven understorey locations (1, 2,...,7) are presented in Fig. 3.3. Bad weather resulted in some missing data. The mean day length during the field study was about 12 hours, ranging from 11.77 in 17th March to 12.17 hours in April 21st.

Below-canopy fluxes depended on the weather conditions and canopy openness. The understorey environment exhibited significant spatial variability in the proportion of PPF intercepted by the forest floor (Table 3.1). The average transmittance was 13%. The transmittance at individual locations ranged from 2.9 to 33%. The mean percent PPF transmitted at the gap edge was, on the average, 4 times greater than the understorey. When PPF percent transmission is compared in terms of low and high PPF days, low PPF days values were generally high (Table 3.1). However, none of these differences were significant (P>0.05; Student's t-Test).

The range and distribution of mean daily average PPF in the open, gap edge and locations beneath the canopy are summarized in Table 3.2. Daily average PPF was from 23 μmol m^{-2} s^{-1} in the relatively closed canopy (location 6) to over 1000 μmol m^{-2} s^{-1} in the open. Considerable day-to-day variation was found in each location, depending on the amount and timing of cloudiness (Table 3.2). The coefficient of daily variation was higher in the understorey than at the open, while the gap edge was intermediate in variability. Examples of diurnal trends are given in Fig. 3.4.

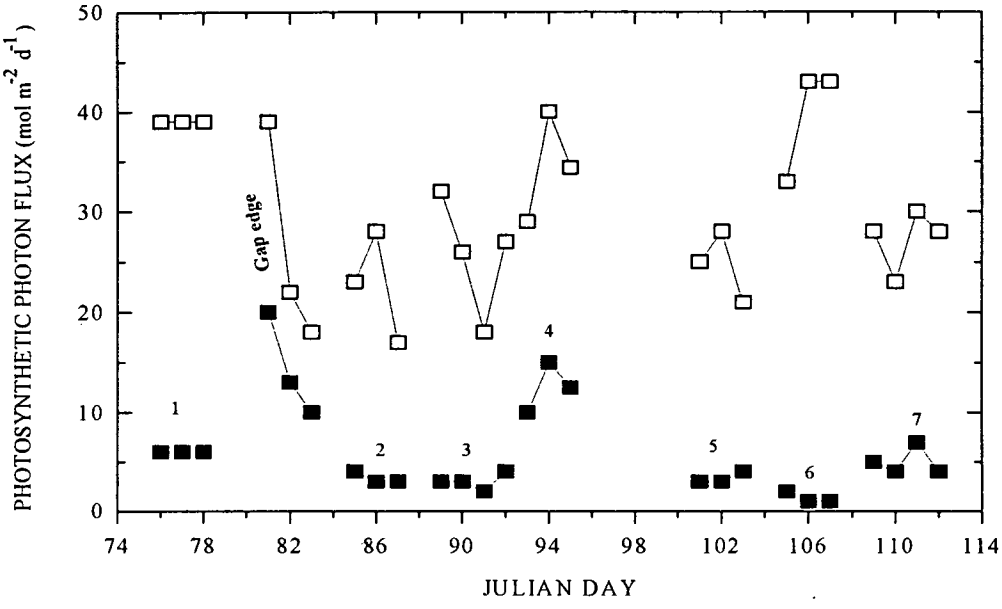

Figure 3.3: Total daily photosynthetic photon flux (PPF) of the open (▫) and eight understorey locations (▪) of the *Juniperus-Afrocarpus* forest stand of Arba-gugu forest at Sengo-kone. Numbers 1 to 7 and 'gap edge' indicate the different locations within the forest. Each datum point is the total of 12 hours observation during March/April 1991. Measurements were taken as described in the text. See also Appendix 3.1.

Table 3.1: Summary of PPF transmission obtained at the forest floor. Values are mean percent open PPF transmitted to the forest floor computed for 6 hours centred at noon (mol m^{-2} d^{-1}). *F*-statistics for one-way ANOVAS for variation among understorey locations are given. $n = 7$; CV = percent coefficient of variation. See also Appendix 3.1.

Location	Mean±SE	CV	Percent PPF of High PPF day	Low PPF day
Gap edge	54.6±2.5	7.9	49.9	55.5
Understorey:				
1	10.9±0.2	2.7	11.2	10.6
2	8.7±0.3	6.1	9.0	9.1
3	11.3±0.7	12.5	9.9	10.4
4	33.1±0.3	1.8	33.6	32.5
5	12.0±1.8	29.3	8.0	16.5
6	2.9±0.8	46.6	1.9	4.5
7	15.5±1.4	18.5	19.3	15.6
F-statistics(*P*-value)	62.86(0.000)			

Table 3.2: Summary of daily average photosynthetic photon flux (PPF) and mean percent coefficient of daily variation (CV). Open values are values found for the relevant dates when PPF was measured at the same location in the understorey. *n* is number of days observed at each location.

Location	Daily Average PPF (μmol m^{-2} s^{-1})				Mean daily CV (%)		*n*
	Open		Understorey		Open	Under-	
	Mean	Range	Mean	Range		storey	
Gap edge	611	412-907	324	227-449	42.6	35.4	3
1	910	907-912	105	102-109	0.2	2.6	3
2	534	405-660	50	42-63	23.9	22.3	3
3	595	426-745	72	51-83	21.8	19.6	4
4	797	671-921	257	208-306	15.6	18.7	3
5	626	495-778	72	63-81	19.3	10.9	4
6	925	771-1002	29	23-39	14.3	28.9	3
7	626	525-683	97	79-130	11.0	23.6	4

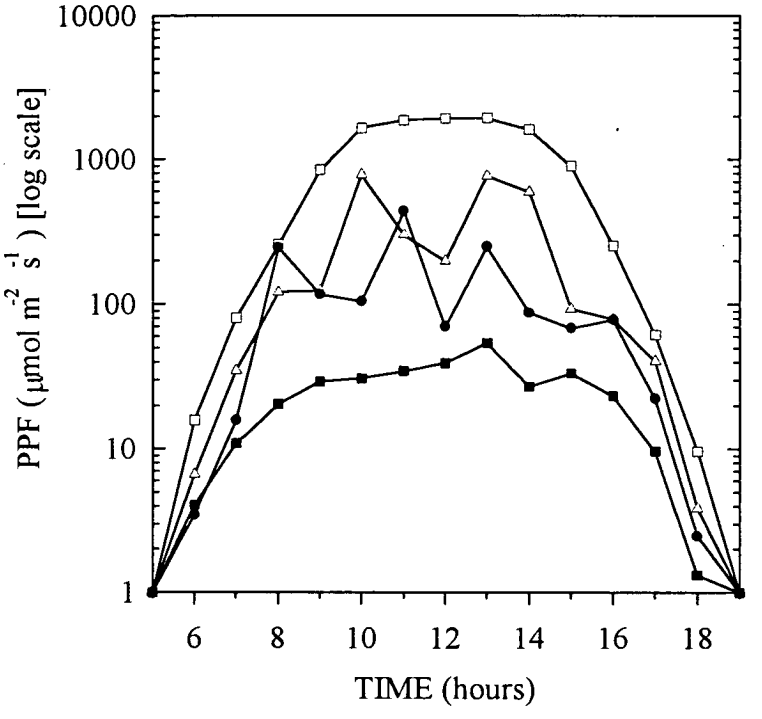

Figure 3.4: Log plot of the diurnal pattern of photosynthetic photon flux (PPF) in *Juniperus-Afrocarpus* forest in Arba-gugu for three clear sunny days in the open (▫), and in the understorey of open density (△), medium density (•) and high density (▪) canopies during March/April 1991. Data points are means of 10-second readings over 1-hour period and each datum point is plotted at the end of the period.

ii) Hemispherical photography results

Percentage canopy gap (gap fraction) of the understorey locations varied by a factor of about 2 with a mean 14.8±1.7% for all locations, while it was 31% and 63% for the gap edge and open (large clearing) respectively (Fig. 3.5). The photographs of the understorey locations clearly demonstrate a greater light contribution from low-angle lighting (Fig. 3.5c) due to disturbance.

In the open, daily PPF was 4.7, 43.5 and 48.3 mol m^{-2} d^{-1} for diffuse, direct and global PPF respectively as predicted from analysis of the hemispherical photographs. Paired comparison of predicted and measured daily total PPF in the open indicate that, the measured daily total PPF obtained from quantum sensors was significantly lower than predicted global PPF (t = 5.37; d.f. = 7; P = 0.001). The measured PPF in the open was, on the average, 68±4% of potential radiation. This difference may be accounted largely to the cloudy weather condition that prevailed during the measurement period. The estimated influence of clouds on incoming radiation are given in Table 3.3.

Table 3.3: Estimate of cloud influence on incoming radiation, calculated from daily measured PPF (mol m^{-2} d^{-1}) as a percent of radiation estimated (cloudless skies) from hemispherical photographs.

Location	Mean	Min	Max	n
Open	32±4	5	59	26
Gap edge	47±10	34	67	3
Understorey	34±5	1	76	24

In the understorey, the mean predicted diffuse, direct and global PPF calculated for dates on which the PPF was measured were 0.94±0.12, 4.3±1.2 and 5.2±1.4 mol m^{-2} d^{-1} respectively. The global PPF was generally higher than the measured PPF. However, paired comparisons of the predicted with measured PPF in the understorey show no significant difference (Student's t-Test; P>0.05, n = 8).

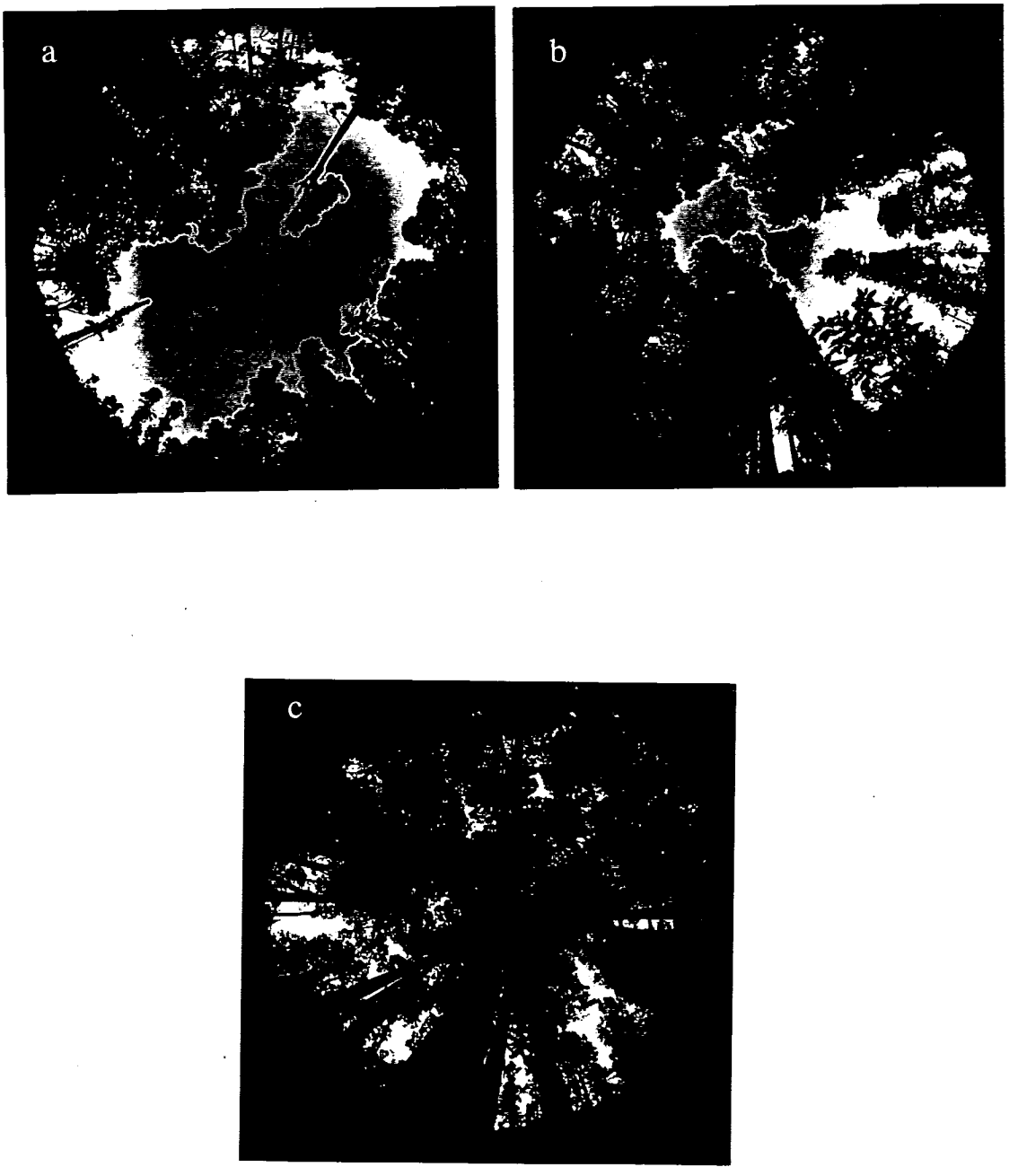

Figure 3.5: Hemispherical photographs showing canopy transmitivity under *J. procera* and *A. gracilior* forest stand at Sengo-kone, Arba-gugu forest. (a): Large clearing (open); (b): gap edge canopy; (c): understorey canopy.

Measured daily total PPF in the understorey was highly correlated with predicted total daily PPF (Fig. 3.6a), and with potential number of sunflecks per day (Table 3.4). Hourly PPF calculated from photos were poorly correlated with hourly measured values.

Table 3.4: Regression statistics for comparison between measured PPF (mol m^{-2} d^{-1}) and radiation components predicted from hemispherical photographs. For all tests, $n = 8$

Comparison (Y x X)	R^2	slope	Intercept
Global transmission percent (Y) Vs:			
Measured percent PPF	0.86	1.53	-7.31
Potential number of minutes of sunflecks per day (Y) Vs:			
Measured PPF	0.95	17.61	-35.15
Measured percent PPF	0.82	6.08	-37.36
Percentage canopy gap (gap fraction)	0.83	13.87	-160.73

On the average, diffuse and direct site factors at the forest floor were 10.0±1.3% and 11.4±3.1% for dates on which light measurements were made (Table 3.5). The predicted PPF transmission was higher than measured PPF transmission at the gap edge but lower in the understorey. This is because actual total PPF will be higher due to light transmitted and reflected downwards by leaves. However, paired comparison shows no significant difference (Student's t-Test; $P > 0.05$, n = 7).

Measured percentage PPF transmitted to the forest floor was highly correlated with global transmission and potential number of minutes of direct sunshine (Table 3.4). Percentage canopy gap (gap fraction) was highly correlated with percentage PPF transmission (Fig. 3.6b) and with potential number of minutes of sunflecks per day (Table 3.4).

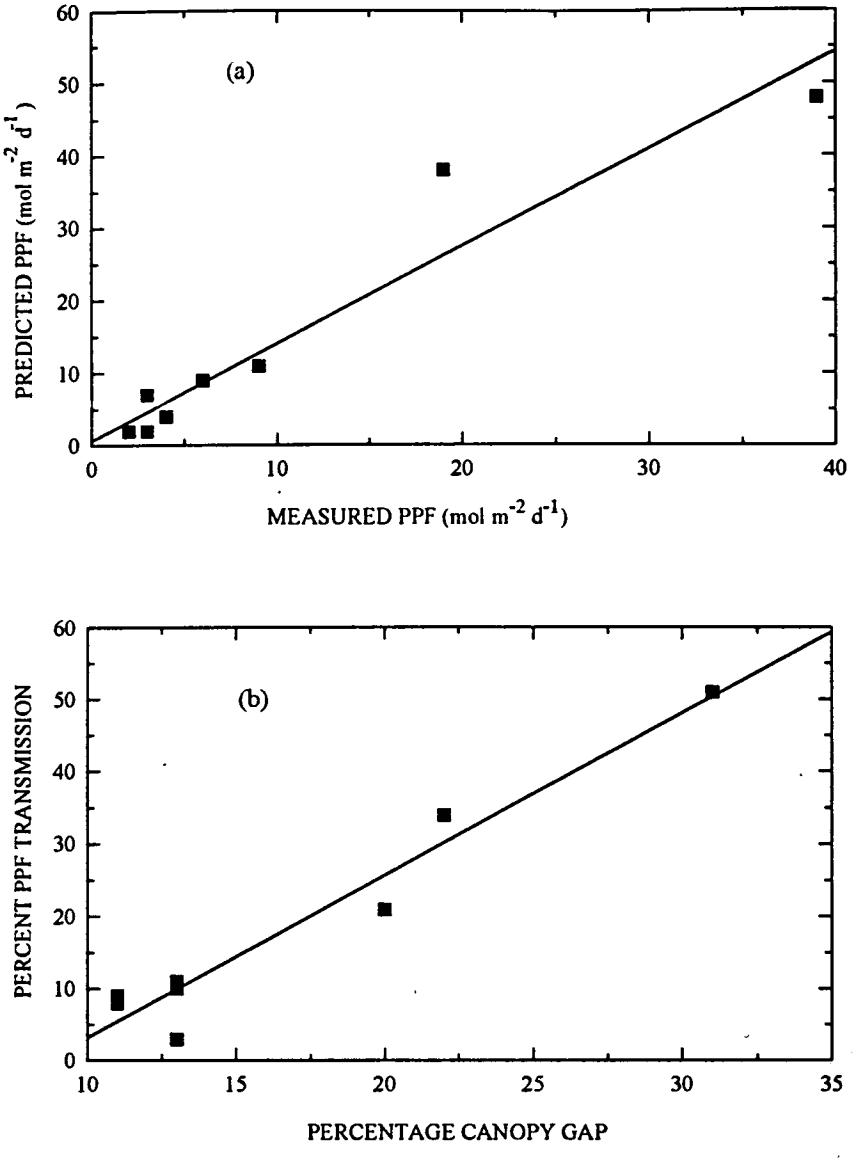

Figure 3.6: Relationship between measured PPF obtained from quantum sensors and predicted PPF and canopy gap obtained from hemispherical photographs. a) Predicted and measured daily total PPF (mol m-^{2} d^{-1}) for nine *Juniperus-Afrocarpus* forest microsites (open, gap edge and understorey locations) ($R^2 = 0.96$; slope = 2.00; intercept = -3.03). b) Empirical model linking measured photosynthetic photon flux (PPF) percentage transmission to percentage canopy gap in Arba-gugu *Juniperus-Afrocarpus* forest ($R^2 = 0.95$; slope = 2.31; intercept = -20.51). Photographs were taken in the same locations where measurements were made. PPF was predicted for the dates of the measurement.

The total PPF received as diffuse was 23.9±4.6% of the total light penetrating through the forest canopy in the understorey locations (Table 3.6). The estimated mean potential number of minutes of sunflecks per day for the same periods was 35.4±7.9 min for all understorey locations, with an eightfold spatial variation between the closed and open canopy locations (Table 3.6). Subtraction of the estimated diffuse light contribution from the measured PPF values obtained from quantum sensors suggests that an average of about 70.4 (ranging from 33.3-85.9%) of the total photon flux in the understorey over the measurement period was due to sunflecks (Table 3.6).

The mean yearly daylength estimated from the photographs was 12.02 hrs, ranging from about 11.5 in December to 12.5 hrs in June.

Table 3.5: Values for diffuse and direct site factors obtained from hemispherical photographs and measured percent PPF transmission for the day PPF was measured.

Location	Diffuse site factor	Direct site factor	Measured percent PPF transmission
Open	50.1	99.6	100
Gap edge	24.5	90.8	51.1
Understorey:			
1	8.6	8.1	10.8
2	6.8	2.7	7.8
3	6.8	4.9	8.9
4	16.5	22.8	33.7
5	9.8	15.4	9.7
6	9.2	2.1	3.2
7	12.4	15.6	20.5

Yearly estimates of the proportion of diffuse PPF to global PPF for the open gave 13.2±1.0% on the average, while it was 16.0±2.1% for the gap edge. Generally, a higher proportion of direct radiation reached in the understorey than diffuse radiation. Diffuse radiation below canopy was about 17.7±1.6% of global radiation, ranging

from 6.1 to 43.5% (Table 3.6). Yearly trends in PPF transmission are shown in Table 3.7.

Table 3.6: Summary of number of minutes of sunflecks per day, percent of diffuse PPF to global and percent contribution of sunflecks for measured daily photosynthetic photon flux (PPF).

Location	Sunfleck per day (minutes)	diffuse as % of global	Measured PPF in sunflecks as % of total PPF
Gap edge	375	6.1	83.5
Understorey			
1	24	20.0	82.3
2	12	36.9	70.1
3	20	25.3	79.2
4	80	14.4	85.9
5	52	13.6	70.0
6	8	43.5	33.3
7	52	13.7	72.0

The yearly mean potential number of minutes of sunflecks per day estimated from 25 solar tracks was 39.5±1.5 for all understorey locations (Table 3.8). The mean values of potential number of minutes of sunflecks per day for all understorey locations for individual days (solar track) ranged from 26 to nearly 55 min. The mean values for the individual understorey locations for all solar tracks, ranged from 19.3±2.4 to 82.0±9.7 min. Values for individual locations for an individual day (1 solar track) ranged from no sunflecks, where the sun path was obstructed for the whole day, to 191 min (location 4). However, a location that had the highest value on one day did not necessarily have the highest on another. This is because the occurrence of a sunfleck depended on the alignment of the sun and the configuration of the canopy gap. The coefficient of variation for monthly estimate of the potential number of minutes of sunflecks per day at each location was high (Table 3.8). The *F*-statistics indicates a significance variation between locations, while no significant variation was found between months ($<P$ 0.05).

Table 3.7: Descriptive statistics for yearly and monthly estimate of direct site factor (%) for the understorey locations obtained from hemispherical photographs. Yearly values of each location are results of 7 months (December to June) calculated from 25 solar tracks (every quarter month) from 21st December to 21st June. The monthly values are from 4 solar tracks except December which was from 1 solar track. *F*-statistics for one-way ANOVA for variation among locations are given. $n = 7$. See Appendix 3.2 for estimated radiation.

a) Yearly estimate:

Location	Mean	SE	CV
1	6.1	0.53	23.2
2	9.1	2.93	85.2
3	3.8	0.76	52.7
4	22.3	3.38	40.2
5	12.4	2.46	52.4
6	10.5	3.93	98.7
7	13.6	1.98	38.6
F-statistics(*P*-value)	5.41 (0.000)		

b) Monthly estimate:

Month	Mean	SE	CV
December	12.0	3.08	67.7
January/November	13.2	2.68	53.8
February/October	12.2	2.07	45.1
March/September	9.8	2.95	79.4
April/August	7.6	2.96	103.1
May/July	11.2	4.08	96.6
June	11.9	4.86	108.4
F-statistics(*P*-value)	0.31 (0.929)		

Table 3.8: Descriptive statistics for yearly and monthly estimate of potential number of minutes of sunflecks per day for the understorey locations. *F*-statistics for one-way ANOVAS for variation among locations are given. $n = 7$

a)Yearly estimate:

Location	Mean	SE	CV
1	19.3	2.4	61.9
2	23.4	3.7	80.1
3	14.7	1.9	63.1
4	82.3	6.9	42.2
5	51.0	5.7	56.2
6	33.1	6.7	101.1
7	52.9	4.8	45.8
F-statistics(*P*-value)		5.97 (0.000)	

b) Monthly estimate:

Month	Mean	SE	CV
December	44.0	9.9	59.3
January/November	47.1	9.8	55.0
February/October	44.9	7.7	45.3
March/September	36.6	10.8	78.2
April/August	27.2	10.3	100.3
May/July	39.4	14.6	97.7
June	42.5	16.4	101.8
F-statistics(*P*-value)		0.33 (0.916)	

It is important to notice that monthly and yearly estimates of the direct site factor and potential number of minutes of sunflecks at quarter month intervals from 21st December to 21st June calculated from 25 solar tracks (Table 3.7; 3.8) as opposed to only 7 solar tracks, has given a better picture of the direct radiation input at each location than the estimate made from one solar track (single day) on the day PPF was measured at that location (Table 3.6). This effect becomes more obvious by comparing the relationships of the percentage canopy gap with potential sunflecks in Table 3.4 and Table 3.9.

The yearly estimate of sunfleck duration calculated from 25 solar tracks for each location from the photographs for seven understorey locations averaged 5.6±0.6 min, with the mean ranging from 3.5 to 7.8 min. In all locations, potential sunfleck duration was very brief with a median duration of 2-4 min, and a modal class of 2-3 min. Frequency distribution of the properties of sunflecks (Fig. 3.7) illustrates that the most frequent class was from 1 to 3 min in duration accounting for 60% of the total sunflecks. Only ~10% of the sunflecks were <1 min in duration, while those >20 min accounted for only 5%. The longest sunfleck (sunpatch) lasted 103 min. These calculations are only for comparative purposes, since clouds and motion by leaves in wind will result in many sunflecks of much shorter duration.

Regression of yearly photographic values of direct and global PPF on measured values using data from all locations revealed a very high significant linear relation (Table 3.9). Seasonal variability in PPF was evident in the clearing. On the basis of calculated values increased solar elevation must have resulted in more direct radiation at solar noon on clear days during the period of measurement (Fig. 3.8) in Araba-gugu forest. This effect is seen in the highest daily total PPF measurements in the open on Julian days 106 and 107 in April (Fig. 3.3). The months of March and April are, however, characterized by more clouds with alternately clear sunny and rainy weather each day.

Table 3.9: Regression statistics for comparison between measured daily total PPF and Predicted direct and global yearly PPF estimate obtained from hemispherical photographs.

Comparison X Vs Y	R^2	slope	Intercept	n
Measured mean PPF Vs:				
Predicted PPF	0.99	480.9	2.05	9
Percentage canopy gap Vs:				
Global transmission	0.98	366.7	-7.06	9
Potential sunflecks per day	0.99	548.6	-54.07	9
Sunflecks duration Vs:				
Potential sunflecks per day	0.002	0.009	54.70	7

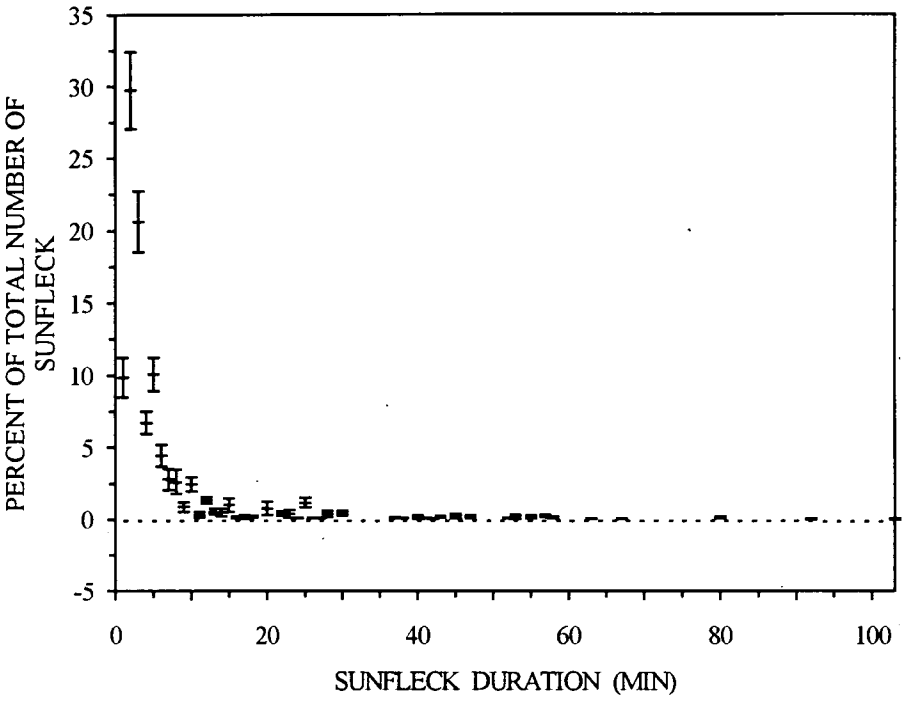

Figure 3.7: Frequency distributions of potential sunfleck duration under *Juniperus-Afrocarpus* forest stand. The bars represent the means (±SE) of the percentage of total number of sunflecks received. $n = 7$.

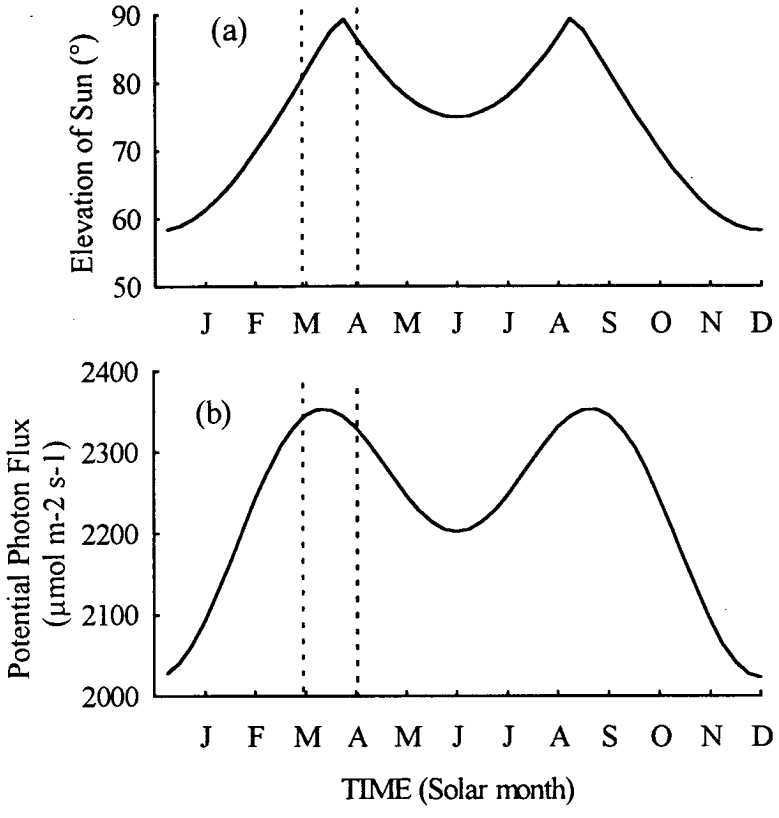

Figure 3.8: Annual changes in (a): solar angle; and (b): potential photon flux, at solar noon 8° 20' N. Solar constant of 2510 µmol m^{-2} s^{-1} is assumed. The monthly values are plotted 21st day of each month. The vertical dotted lines indicate the period of the field measurement. Elevation of the sun and potential photon flux were calculated as described in the text.

iii) Microsite variation in Red:Far-red ratios (R:F-r)

The mean daily R:F-r ratio in the open measured for six days was 1.25±0.10, while it was 0.61±0.05 in the understorey, when the mean daily total PPF was 34.7±2.9 and 6.7±1.2 mol m^{-2} d^{-1} respectively (Table 3.10). There was no significant differences in the R:F-r ratio between the open, medium and closed canopies (Table 3.10). The diurnal pattern of R:F-r ratio and PPF, in the open and in the understorey are given in Fig. 3.9. R:F-r ratios were highly correlated with PPF (open: $R^2 = 0.92$; understorey: $R^2 = 0.89$)

Table 3.10: Summary of Red:Far-red ratios, daily photosynthetic photon flux (PPF) and percent open PPF transmission of the open and forest understorey (open, medium and closed canopy density) during December 1992. Mean of 6 days observation. ranges are given in parentheses. *Mean of 12 spot measurements from 7:00am to 6:00pm.

Variable	Open	Open canopy	Medium canopy	Closed canopy
Daily total PPF (mol m^{-2} d^{-1})	34.7 (18.6-39.2)	10.0 (1.4-18.8)	6.7 (0.68-9.1)	3.5 (0.12-4.3)
Daily Average PPF (μmol m^{-2} s^{-1})	804	232	154	81
Red: Far-red ratio	1.25 (1.11-1.37)	0.67* (0.58-0.78)	0.62* (0.55-0.69)	0.54 (0.47-0.56)
Percent PPF transmission	100	29.1	12.4	5.2

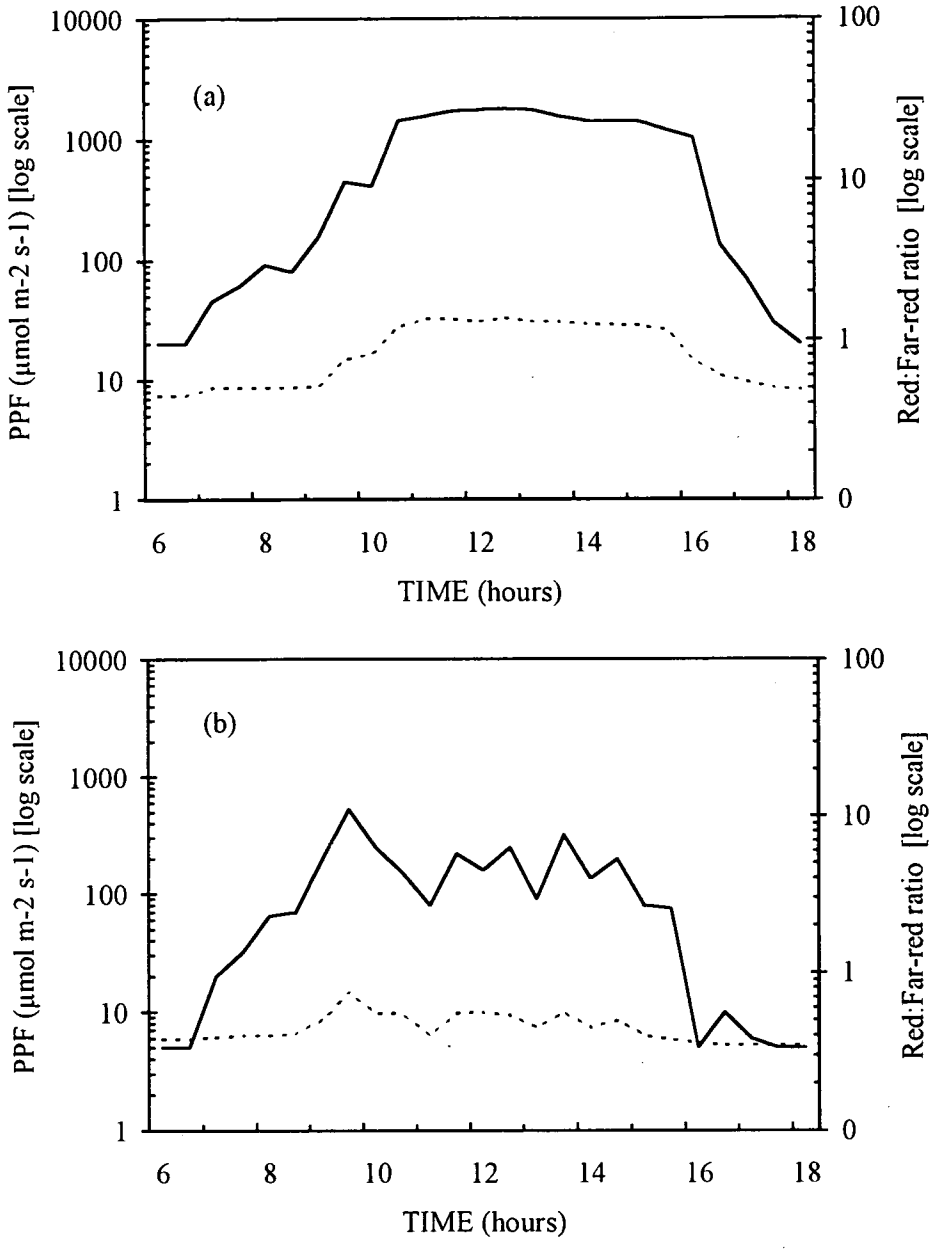

Figure 3.9: Log plot of PPF (µmol m^{-2} s^{-1}) (solid line) and R:F-r ratios (dotted line) of the open (a) and understorey location (b) in Arba-gugu *Juniperus-Afrocarpus* forest at Sanka-Meda on relatively sunny days, December 14 (a) and 16 (b) 1992. Data points are means of 10-second readings over 30-min period and each datum point is plotted at the end of the period.

3.4.2 Air temperature

The mean daily (day and night) air temperature in the open averaged 16.7±0.2 °C ranging from 14.7 to 19.8 °C over 27 days in March and April 1991 (Fig 3.10). There was a highly significant positive relationship between the daily mean air temperatures in open and in the understorey (during day: $R^2 = 0.843$; night: $R^2 = 0.903$ $n = 27$). The air temperature in the open, was significantly higher than in the understorey during the day (Paired Student's t-Test: $t = 9.0$, d.f. = 23, $P < 0.0001$), while it was significantly lower than in the understorey locations during night ($t = 4.7$, d.f. = 23, $P < 0.0033$). Paired comparison between day and night air temperatures over 24 days shows a significantly lower temperature during night both in the open and in the understorey (Table 3.11).

Table 3.11: Summary of mean day and night air temperatures (°C) for the open and understorey locations. Paired Student's t-Test was used to assess the level of significance of differences between the open and understorey. For all-test; d.f. = 23.

Location	Mean	Min	Max	t	P (2-tail)
Open:					
Day	19.1	16.3	21.5		
Night	13.8	12.6	15.2		
Understorey:					
Day	17.1	14.9	18.8	17.2	0.0000
Night	14.2	12.6	15.4	13.1	0.0000

The mean air temperature differences between open and understorey both during day and night are presented Table 3.12. It is to be noted that the day-time air temperatures in the open, on the average, was about 3 °C higher than in the understorey, whilst night-time air temperatures, though slightly lower in the open (by about -0.4 °C), were fairly constant both in the open and understorey (Fig. 3.10; Table 3.12).

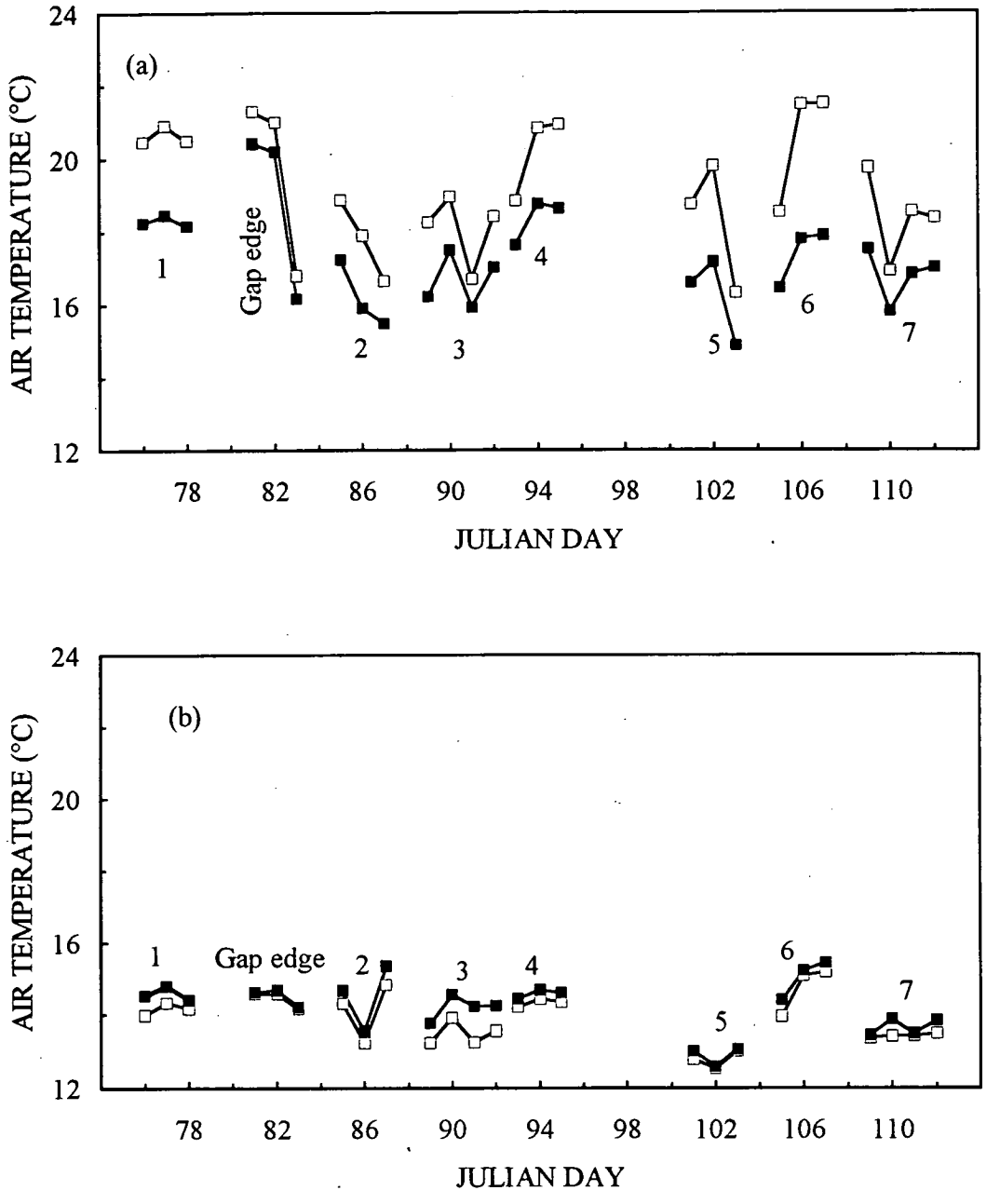

Figure 3.10: (a): Mean day, and (b) mean night air temperatures of the open (▫) and understorey locations (▪) of *Juniperus-Afrocarpus* forest stand of Arba-gugu forest at Sengo-Kone during March/April, 1991. Numbers 1 to 7 and 'gap edge' indicate the different locations within the forest. See also Appendix 3.3.

Table 3.12: Summary of mean air temperature differences (°C) between the open and understorey locations during day and night. The difference was calculated from seven hours data centred at noon to avoid the shading effect of trees in the open.

Location	Clearing (-) Understorey		Day (-) Night	
	Day	Night	Clearing	Understorey
Gap edge	1.3	0.0	7.3	6.0
1	3.9	-0.6	10.3	5.9
2	2.3	-0.5	7.9	5.0
3	2.3	-0.7	6.9	3.9
4	2.4	-0.3	7.9	5.1
5	2.9	-0.1	7.2	4.2
6	4.6	-0.3	9.0	4.1
7	2.3	-0.2	7.3	4.8

The difference in the gap edge was lower than in the understorey during day, while there was no difference during night. The day time air temperature in the open, on the average, was higher by 8.1 °C higher than night, while it was higher by 4.7 °C in the understorey.

The spatial air temperature differences between the lowest and the highest in the understorey locations were 2.1 °C during day and 1.9 °C during night (Fig. 3.10).

Fig. 3.11 illustrates the diurnal pattern of the daily mean air temperatures. Values were obtained from 3 relatively clear days for the seven understorey locations and for simultaneous measurements in the open.

Fig. 3.12 illustrates typical measurements of the spatial air temperatures in an understorey and open in relation to the input of radiation. It is important to notice that the air temperature difference between the open and understorey (Fig. 3.12b) follows the diurnal pattern of the open radiation input (Fig. 3.12a). There is a time lag between the maximum radiation input and maximum air temperature. The hourly mean daytime air temperature difference of the open location and seven locations underneath the canopy was highly correlated with the diurnal PPF pattern of the open

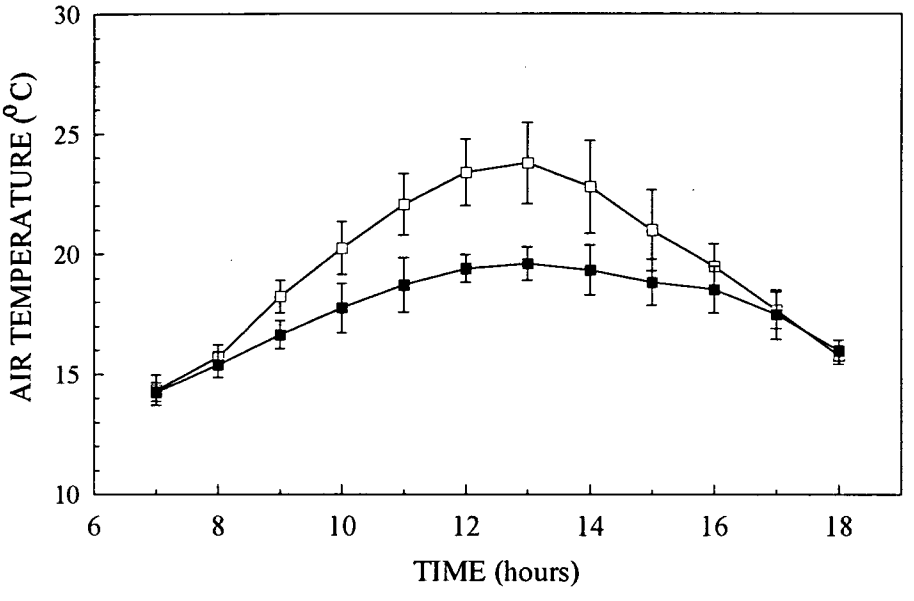

Figure 3.11: Mean daily pattern of air temperatures of open (▫) and eight understorey locations (▪) of *Juniperus-Afrocarpus* forest stand of Arba-gugu forest at Sengo-kone during March/April, 1991. Each understorey datum point represents the means of 3 day's observation at each of the understorey and the 'gap edge' locations and 23 days observation for the open site. The bars represent the (±SE) of the mean. Measurements were taken as described in the text.

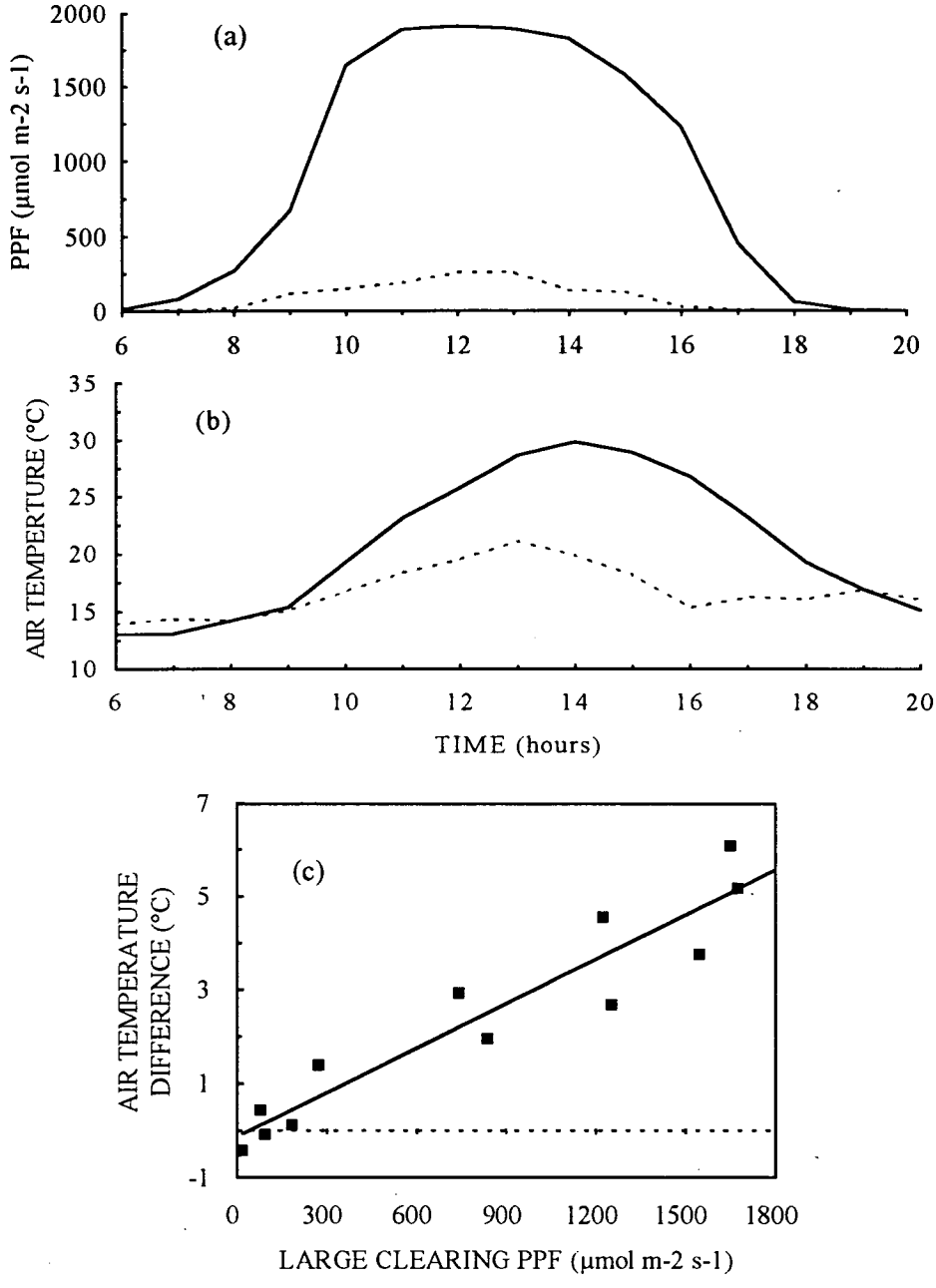

Figure 3.12: Variation in air temperature in the open and understorey (location 1 on Julian day 77) in relation to daily net radiation input in clear sky conditions. a: Net PPF (radiation) measured in a open (solid line) and beneath a forest canopy (dotted line); b: Air temperature measured at the same location; c: Relationship between hourly mean PPF of the open and hourly mean day air temperature difference of the open and understorey ($R^2 = 0.89$). Each datum point of Fig. (c) is the mean of 3 days observation at each of the seven locations during March/April 1991.

(Fig. 3.12c; $R^2 = 0.89$). The value of R^2 for the individual locations ranged from 0.78 to 0.95 (Table 3.13). The regression was computed from one relatively clear day for each location. There was a significant linear relationship between the daily total PPF and mean daily air temperatures both in the open and in the understorey (open: $R^2 = 0.78$, $n = 26$; understorey: $R^2 = 0.70$, $n = 23$).

Table 3.13: Regression statistics comparing PPF input at the open, and open minus understorey hourly air temperature differences. (PPF = X, and temperature difference = Y) For all-tests; $n = 12$

Location	R^2	Intercept	Slope
1	0.95	-0.843	0.004
2	0.95	0.067	0.003
3	0.94	-0.065	0.003
4	0.78	-0.104	1.071
5	0.91	0.352	0.004
6	0.79	-0.047	0.004
7	0.85	-0.117	0.003
Mean value	0.89	-0.129	0.003

3.4.3 Soil moisture contents

The soil moisture content in the open (Table 3.14) was 27.8±2.0% of the oven dry weight for all samples, while the mean soil moisture content underneath the canopy was 27.9±1.1% for all samples for all locations. The F-Test (one-way ANOVA) for the different samples confirms a significant sample-to-sample variation ($F = 7.53$; $P < 0.00$; d.f. = 7). There was, however, no significant spatial variation between locations underneath the canopy. Paired (Student's t-Test; $P < 0.05$; d.f. = 7) comparison reveals no significant difference in the mean soil moisture contents between the large clearing and understorey locations.

There were no relationships between soil moisture and canopy gap, PPF or air temperatures for the large clearing or for any of the understorey locations (Table 3.15). This is probably, in part, due to varied irregular weather conditions

throughout the period of the field study with alternately clear, cloudy and/or rainy periods, and in part, that soil moisture is controlled by other factors such as topography, wind and precipitation other than light and air temperature alone.

Table 3.14: Summary of gravimetric soil moisture content (%) of the oven dry weight of *J. procera-A. gracilior* forest stand in the large clearing and understorey locations of Arba-gugu forest. Paired Student's *t*-Test was used to test the level of significance of differences with the clearing. For all tests, d.f. = 7.

Location	Mean	SE	CV	*t*	*P* (2-tail)
Clearing	27.8	2.0	20.8		
Gap edge	25.0	1.7	19.0	-2.6	0.034
Understorey:					
1	28.0	1.9	19.1	0.4	0.705
2	22.8	2.8	35.3	-3.9	0.006
3	25.7	2.7	30.1	-1.7	0.135
4	30.4	1.6	15.0	3.4	0.012
5	30.5	1.9	17.8	5.3	0.001
6	27.5	1.7	17.7	-0.3	0.756
7	30.5	1.9	17.2	4.3	0.004

Table 3.15: Regression statistics comparing soil moisture contents with observed photosynthetic photon flux (PPF), gap fraction and air temperature of the Arba-gugu *J. procera* and *A. gracilior* mixed forest stand. For all-tests; $n = 8$.

Comparison (Soil moisture Vs *X*)	R^2
Large clearing PPF	0.007
Understorey PPF	0.002
Percent PPF transmission	0.004
Canopy gap fraction	0.014
Large clearing air temperature	0.058
Understorey air temperature	0.063

3.5 Discussion

3.5.1 Analysis of the method

Overall, predicted PPF based on values obtained from hemispherical photographs were closely correlated with measured values over a range of radiation conditions (Table 3.4 and 3.9; Fig. 3.6). However, attention should be drawn to differences in the relationship of percentage canopy gap (gap fraction) with percent open PPF transmission (Fig. 3.6b) and with number of minutes of sunflecks per day (Table 3.4) especially in low-light locations where proportional differences were sometimes large. These differences, though not statistically significant, are probably due to the short-term nature of the measurements used (single day).

Caution must also be exercised when reporting radiation flux as a percentage of open/above-canopy PPF, because different results are obtained depending upon whether instantaneous or daily totals measurements in the open are used as a reference (Rich *et al.*, 1993). In the present study, percentage transmittance values (Table 3.1 and 3.5) are not directly comparable with instantaneous measurements and are based on 6 hours daily total PPF centred at noon.

Differences between measured and predicted global PPF transmission and direct site factor probably resulted from combined effects in the imaging and evaluation system including image distortion, insufficient resolution of small-scale canopy features, mis-identification of open and closed areas, and minor differences between photo and sensor locations. The lower predicted global transmission relative to measured, although not statistically significant, probably reflects penumbral effects which become more important as the apparent size of the sun's disc becomes large relative to the size of canopy openings (Anderson. and Miller 1974). The analysis in the present study assumes sun is a point source.

Estimation of the monthly and yearly direct site factor and potential number of minutes of sunflecks at quarter month interval from 21st December to 21st June from 25 solar tracks (Table 3.7; 3.8), as against from only 7 solar tracks, gave a

representative value of the direct radiation input at each location. This was because a location that had the highest value on one day within a month did not necessarily have the highest on another, and it depended on the alignment of the sun and the canopy gap.

Another parameter that may greatly affect in the estimation of PPF is the sampling and averaging of PPF measurements. In the this study, measurements were taken every 5 minutes and stored as 1-hour averages, due to the limited storage locations in the data logger. Thus, the duration of sampling and 1-hour averages have undoubtedly obscured much of the diurnal short-term variation particularly in the understorey, where the light intensity is very variable with short periods of intense light in sunflecks.

In conclusion, a considerable portion of the differences between prediction and measurements can be accounted for by errors in the measurements. Taking all of the above possible sources of errors into account, predicted PPF and estimated radiation components obtained from hemispherical photographs were highly correlated with measured values obtained from quantum sensors (Fig. 3.6; Table 3.4 and 3.9). Hence, the overall pattern of radiation distribution could be compared between measured and predicted. Moreover, such strong correlation between measured and predicted radiation components indicate that estimates of light availability from hemispherical photographs can provide a powerful and a general approach to quantifying many aspects of the forest light environment under study. Also, the empirical calibration developed in this study (Fig. 3.6b) will allow refined prediction of PPF and meaningful regeneration microsite comparisons from hemispherical photographs. Such calibration does not affect the ability to make relative comparison between photographs. In the absence of any long-term monitoring of PPF with quantum sensors, hemispherical photographs have been used successfully in a broad range of studies involving microsite characterization of solar radiation regimes (e.g. Pearcy, 1983; Chazdon and Field, 1987; Vales and Bunnell, 1988; Lee, 1989; Turner, 1990; Canham *et al.*, 1990; Rich *et al.*, 1993).

3.5.2 The Light Environment

i) Photosynthetic photon flux (PPF)

The variability in the light environment within and between the nine locations can be interpreted on day-to-day, diurnal and seasonal time scales. On a day-to-day basis, the open (large clearing) and the seven understorey locations were very similar (Table 3.2). The gap edge was intermediate in variability at both time scales.

Although the methods and equipment used by different workers to measure relative irradiance varied a lot there was a general similarity in the values that were measured and reported for the forest floor of tropical rainforests by other authors. Values of <1% was reported by McLean (1919), Carter (1934). Values between 1 - 5% were reported for different tropical moist forests by Allee, (1926), Evans (1956), Whitmore and Wong (1959), Schulz (1960), Pearcy (1983), Chazdon and Fetcher (1984), Torquebiau (1988), Canham *et al* (1990) and the closed canopy stations in Costa Rica by Rich *et al* (1993).

Canham *et al* (1990) using hemispherical photography, also reported 0.6%, 1.3% and 1.3% global PAR transmission respectively for Douglas-fir - hemlock forest in the Cascade Mountains, northern hardwood forest in southwestern Ohio and southern hardwoods in southeast Ohio, all in the United States. Light levels reported in most of the above studies are apparently considerably lower than in Arba-gugu forest, since less than 5% of the PPF above-canopy, reached the forest floor compared to values of 2.9-33.1% (Table 3.1) in this study. It is comparable to at least the small gap stations mean transmission value of 9-10% in primary tropical wet forest in Costa Rica (Rich *et al.*, 1993), and 5.2% in spruce - balsam fir forest in Great Smoky Mountain National Park, in the United States (Canham *et al.*, 1990), and 16.5% with a range 2.6 to 56.7% reported for the coniferous forest stand in Vancouver Island, British Columbia, Canada (Vales and Bunnell, 1988).

Sunflecks were not measured, but the analysis of the fish eye photographs (above) gives insight into the way in which the PPF measured at the ground may be distributed on sunny days. This distribution pattern (Fig. 3.7) may be characteristic of the leaf

size and clumping, and is of considerable theoretical interest. However, little comparable data from other forests are available in the literature, and very few studies have reported the plant response to sunflecks (Pearcy, 1983).

Despite the tremendous variation in sunfleck characteristics within the forest considered in this study, and its difference from almost all tropical and subtropical rainforests and some of the temperate forests described above, the percentage of total PPF contributed by sunflecks is estimated to be similar to that found in tropical rainforests (e.g. Evans, 1956; Whitmore and Wong, 1959; Grubb and Whitmore, 1967; Pearcy, 1983, 1987; Chazdon, 1986; Lee, 1987 and Canham *et al.*, 1990) and temperate coniferous forests (e.g. Reifsnyder *et al.*, 1971; Powels and Björkman, 1981; Weber *et al.*, 1985; and Canham *et al.*, 1990).

ii) Red:Far-red Ratios

R:F-r ratio of 0.5 to 0.7 obtained in the *J. procera* and *A. gracilior* forest understorey in the present study (Table 3.10), is like temperate and boreal coniferous forests (e.g. Federer and Tanner, 1966), rather than broad leaved forests (e.g. Stoutjesdijk, 1972b; Turnbull and Yates, 1993). This result, generally agrees with the fact that spectra underneath coniferous forests have a more uniform distribution (Morgan and Smith, 1981a).

3.5.3 Air Temperature

The air temperature patterns observed within the understorey and in the open in this study, show similar trends to those reported by Longman and Jenik (1974) for a forest in southwestern Ghana and by Cole (1980) for Gola forest in Sierra Leone. Nevertheless values are not directly comparable due to differences in method of measurement, seasons, altitude and general character of the forest. However, the daily mean air temperature values found in this study are within the range of the values reported for the species in the natural environment (White, 1983; Hall, 1984). Both the open and the forest understorey locations are characterized by significantly high day and low night air temperatures. The open site was significantly warmer during the day and cooler at night compared to the air temperature underneath the canopies

(Fig. 3.10; Table 3.12). It is probable that the day-time air temperature in the understorey is moderated in two ways: firstly, the leaves in the canopy intercept most of the solar radiation keeping it from the forest floor; secondly, the temperature in the understorey is moderated through transpiration from the leaves, preventing the day-time temperature from rising rapidly as in the open (e.g. Wenger, 1984). At night the temperature is moderated within the forest by long-wave radiation from the canopy which is maintained near to air temperature. This contrasts with night sky which has a very low radiative temperature, leading to a rapid cooling in the open site.

3.5.4 Soil moisture contents

The result of this study has shown adequate soil moisture for the period of the study, both in the open and in the forest understorey (Table 3.15). A higher water use by forests (Packham and Harding, 1982) is expected, particularly forests composed of trees with extensive lateral and deep root systems such as *J. procera* trees. This would give dryer soil profile under forest. On the other hand, surface layers of open soils may become very dry because of direct insolation.

3.6 Conclusion

The combined use of PPF sensors and hemispherical photographs enabled accurate characterization of the microsites and mechanistic understanding of the causes of temporal radiation variability. At day to year scales, it was possible to distinguish variability resulting from seasonal shifts in solar angle, changes in radiation level outside the canopy in the open, and changes in the geometry of canopy opening.

It was also possible to develop a simple empirical model which allows the estimation of PPF in regeneration microsites of the forest from hemispherical photographs. While quantitative predictions are subject to several limitations, relative predictions from the hemispherical photograph analysis yield other advantages. Because such an approach estimates the maximum potential PPF rather than actual PPF, it eliminates the day-to-day variability that causes difficulties with between-site comparisons based on measurements from different dates. For comparisons of light micro-environments

within a region, relative measures of potential PPF provide a robust comparative characterstic obtainable at a single time that can be interpreted for any date and is largely unaffected by weather conditions. By accounting for regional differences in cloudiness and atmospheric transmissivity, the approach could be applied to inter-regional comparisons. However, calibrations in this study are particular to the forest type and range of canopy openings measured.

The heterogeneous distribution of radiation under the examined *J. procera-A. gracilior* forest stands indicates that especially in this type of open-canopied forests the distinction of gaps and non-gaps appears to be an oversimplification, because gaps of different size exists throughout the forest. The measurements of PPF described in this study are presumably on the high side, since PPF measurements were made during the maximum radiation period of the year. However, the percentage PPF transmission obtained from quantum sensors, site factors and the sunfleck duration described here may be representative of much of the forest area.

In summary, the understorey environment of the *Juniperus-Afrocarpus* coniferous forest is characterized by a relatively open canopy and high light with little annual variation, fairly small daily air temperature variation with adequate soil moisture content for the growth of understorey shrubs, tree saplings and seedlings, especially the herbaceous perennials.

At present, a deeper understanding of the ecology and dynamics of the *Juniperus procera* and *Afrocarpus gracilior* is constrained by lack of data on the germination and seedling responses to environmental variability. Field and laboratory research on germination and growth responses to ground preparation, pre-germination treatments and light will provide a basis for the integration of ecophysiological processes and regeneration patterns. The next chapters will focus on such an integration which is essential for the development of the Afromontane coniferous forest management programmes.

CHAPTER 4

Effects of Clearcutting and Ground Preparation on Seed Germination and Natural Regeneration

4.1 Introduction

A brief review on the influence of forest harvesting practices and site preparation operations on regeneration was presented in Chapter one. The importance of ground preparation that exposes mineral soil following harvesting was emphasized for increasing germination density. The uncertainity of successful *Juniperus procera* natural regeneration either under mature stands or after felling was also noted as being a major management concern. Although it is generally accepted that germination is one stage of the regeneration process that may be influenced by gap formation, information concerning the influence of canopy gaps on the *Juniperus procera* and *Afrocarpus gracilior* seed germination is limited. *J. procera* has been described by Gardner (1926) as a strong light demander which does not regenerate where there is any organic material covering. White (1983) and Hall (1984) also describe *J. procera* as regenerating after fire, but there was no particular evidence of increased rates of seedlings establishment in several fire sites when visited during site selection (Chapter 2). There may be some evidence that *J. procera* regenerates on disturbed soils. However, other seedlings also occur in areas of apparently stable soil. This requires further investigation.

The objective of this study is a better understanding of the net effect of seed supply and seedbed changes on seed germination and natural regeneration of the two species. The influences that specific variables such as canopy gap, ground vegetation cover, leaf litter, site preparation or seed dispersal have upon seed germination and natural regeneration need further investigation. Therefore, more field-oriented work is necessary to elucidate the different roles that dispersal, seed germination, and seedling establishment have upon tree regeneration in forest understorey and clearings. It is during these early stages of the regeneration cycle that the greatest mortality occurs; better understanding of these early stages can greatly expand our understanding of the factors that influence tree regeneration in the afromontane coniferous forest.

In this study, factors that promote germination and/or natural regeneration of *J. procera* and *A. gracilior* following clear felling were investigated. There were two field studies: (a) relationships between microsite conditions and the number and/or distribution of *J. procera* and *A. gracilior* natural regeneration; (b) the effects of ground preparations and seed supply on the germination and/or natural regeneration and seedling growth following forest harvesting. The study was undertaken during the short rainy period in March/April 1991.

4.2 Material and methods

4.2.1 Field study 1: Microenvironment of natural regeneration microsites

i) Site selection and description

Four sites with a relatively good natural regeneration and one site with no regeneration were selected to relate the distribution of natural regeneration to microsite. These sites were located in different parts of the Arba-gugu forest described in Section 2.2 with different levels, and history of disturbance:

1. Site 1 was located at Wakentra at an altitude of 2440 m on a north-west facing slope of 20°. The site was burned during 1974 and has regeneration of both *J. procera* and *A. gracilior* with high proportion of the latter.

2. Site 2 was located at Sengo-kone at an altitude of 2520 m on a north-west facing slope of about 10°. The site was logged and stripped by dozer during 1989 and has regeneration of *J. procera* only.

3. Site 3 was located at Sengo-kone at an altitude of 2510 m on a north facing slope of about 15°. The site was burned during 1972 and has regeneration of both *J. procera* and *A. gracilior*.

4. Site 4 was located at Guna at an altitude of 2560 m on a north facing slope of 19° on a road cut. The top soil has been stripped off during road construction in 1967. The site is since heavily grazed and compacted by sheep and cattle. It has good regeneration of *J. procera*.

5. Site 5 was located at Sengo-kone at an altitude of about 2515 m on a north-west facing slope of about 15°. It represent the relatively undisturbed part of the forest and has no natural regeneration of either conifer.

At each of the above five sites one 10 m x 10 m area was measured and demarcated for the study. Each site was divided into 16 plots of 2.5 m x 2.5 m for enumeration of tree seedlings, measurements of PPF transmission, litter depth, percentage grass, forbs and shrub cover. The light environment was characterised from 16 hemispherical photographs taken at the centre of each plot following the method described in Section 3.3.1. Litter depth was measured from 5 locations at the centre and 4 corners of each plot.

ii) Soil seedbank sample

To assess the presence of viable seeds in the soil seed bank of the forest floor one soil seed bank sample was taken from each of the 16 plots from the undisturbed site 5 with no regeneration. The samples were taken from 50 cm x 50 cm quadrats at 0-3 cm depth at the centre of each plot. The samples taken from each quadrat were mixed thoroughly and spread out separately to air dry. Each sample was sieved with 4 and 2 mm sieve to remove litter, twigs and other materials. The sample contained no seeds of *A. gracilior* but seed of *J. procera* and other unidentified species were present. About 250 g of each sample was brought to the University of Edinburgh and kept in a cold room at 3 °C for 10 days before the experiment.

Each sample was spread on germination trays containing equal parts by volume of vermiculite and perlite. The 16 samples were placed in a randomised block design on an experimental bench in a glasshouse and watered daily. Germination was inspected weekly and recorded until the experiment was terminated after 10 months observation.

4.2.2 Field Study 2: The effects of ground preparation on the germination and/or Natural regeneration following felling and timber extraction

i) Site selection and description

Two relatively undisturbed *J. procera* and *A. gracilior* mixed forest stands, with different proportions of the two species from visual observation, were identified and

located at about 5 km apart in the forest. An area of about 1.2 hectare at Sanka-Meda and about 1 hectare at Guna were delineated for clear felling and timber extraction. The size of the stands for clear felling was decided based on the assumption that natural regeneration is secured either from the seedbank or with seeding from adjacent stands. The site at Sanka-Meda was located at an altitude of about 2700 m on north-west facing gentle slope of about 10° dominated by *J. procera* mature and over-mature trees with high proportion of *A. gracilior* young trees, saplings and seedlings, far from villages and access road. The site at Guna was located at an altitude of about 2400 m on south-east facing slope of about 30° dominated by *A. gracilior* of mature and young trees with few over-mature *J. procera* trees, beside a road in the proximity of villages.

ii) Experimental design and treatments

The stands were clear felled, logged and extracted by Etero Sawmill located in the vicinity (Fig. 4.1). This operation removed all stemwood larger than about 20 cm in diameter, leaving the rest as logging waste as was usually done. At the centre of each clear felled site an area of 1600 m^2 (40 m x 40 m) was demarcated for study. The shortest distance measured from the centre to the edge of the clearing (nearest tree) in 4 directions was 41 m, 46 m, 58 m and 74 m at Sanka-Meda and 35 m, 50 m, 50 m and 63 m at the Guna site.

Three treatments (burning, raking and control) were applied in a Latin square design (Fig. 4.2). The demarcated area was divided into three blocks separated from the adjacent area with 3 m wide fire-line. Each plot was 10 x 10 m and separated from others by 2 m wide. A cultivation treatment was then applied within each plot to give a split-plot design. The three ground preparation treatments (1: removal of all logging waste and ground vegetation, and raking or scraping of the seedbed; 2: burning of all logging waste, ground vegetation and litter, and 3: control where the logging waste and ground vegetation was left untouched) were assigned to each plot randomly.

The weather condition at the time of ground preparation was variable with irregular sunny and rainy intervals and the wind was calm. The logging waste and the ground vegetation was green, while the litter and the soil surface was wet. Due care was taken to distribute the logging waste reasonably well and uniform over each plot in the burning treatment and the control. Since the objective of fire treatment was the baring of mineral soil, all the litter, unincorporated organic materials and the logging

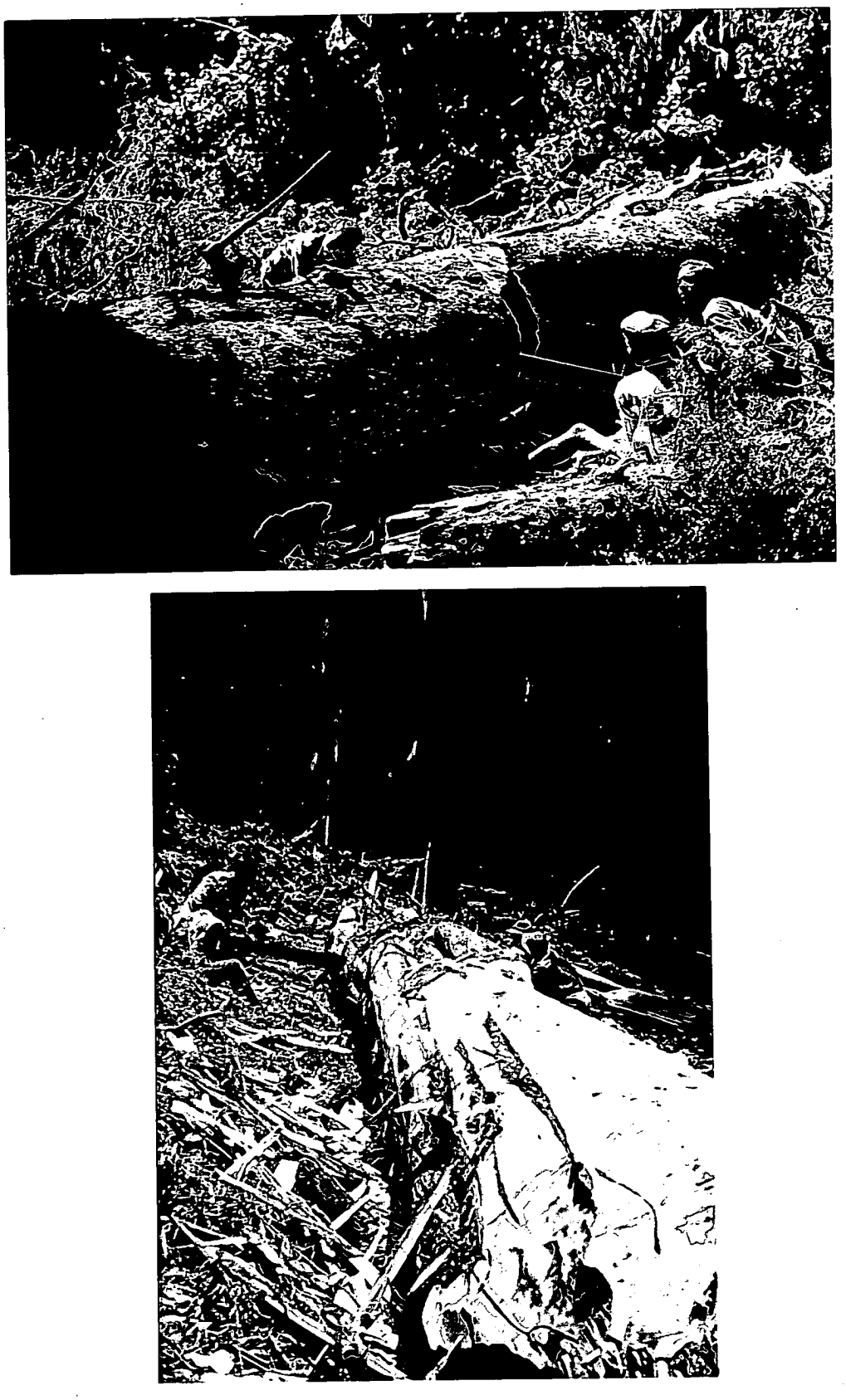

Figure 4.1: Photographs showing the logging operation at Sanka-Meda regeneration experimental site, Arba-gugu forest. *A. gracilior* (upper), and *J. procera* (lower).

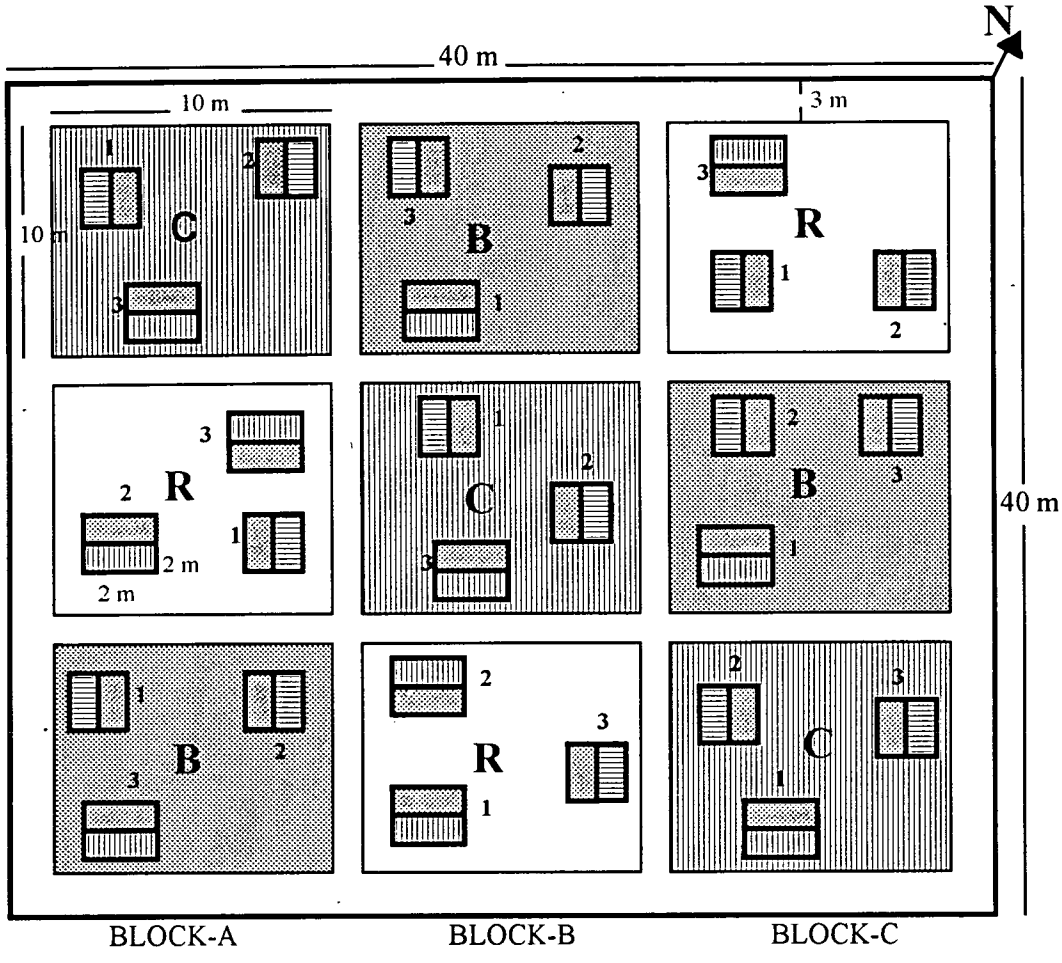

Figure 4.2: Sketch map of *J. procera* and *A. gracilior* artificial and natural regeneration field experiment layout in Arba-gugu forest.

waste were assisted to dry and burned to ash, except for some larger size stemwood which burned only about half way through the stem (Fig. 4.3 lower). Because of the high moisture content, the fire in the burning treatment lasted for about 36 hours. In the raking treatment (mechanical scarification), all the logging waste was collected and carried out of the experimental pot, all ground vegetation was cut and removed, the litter and unincorporated organic matter was totally scraped and removed leaving only bare mineral soil (Fig 4.3, middle). Also, exposed roots of all vegetation visible, except for the tree stumps, on the surface were cut or up rooted and removed.

After the ground preparation three sub-plots (each about 4 % of the plot) of 2 m x 2 m each were established in each plot for shade treatment (no-shade, medium and deep shade). Each sub-plot was further sub-divided into two units of 2 m x 1 m each, each making a seedbed for cultivation and no-cultivation treatments. One of these units was deeply cultivated using a pickaxe to a depth of about 30 cm and raked to form a seed bed in each sub-plot, while the other unit was left uncultivated. As showen in Fig. 4.2, the rest of the area outside the sub-plot in each plot (about 88 % of the plot) was left for natural regeneration observation. In an attempt to get information on the effect of light, three levels of light (80%, 50% and no-shade) were provided using bamboo lathe cover woven together with wire for the three sub-plots in each plot. Fig. 4.4 also shows the general view of the experimental layout.

iii) Seed collection and sowing

Freshly collected fruits of both *J. procera* and *A. gracilior* from the forest were extracted, spread on a canvas to air dry and stored at room temperature for about 3 weeks before sowing. Two hundred seeds of each species were sown in each of the cultivated and uncultivated units by drilling across the bed in April, 1991 (Fig. 4.5). The seeds were covered on whatever loose material was available in each plot. However, it was not possible to cover the seeds in the uncultivated units, particularly in the raking treatment, due to the problem of finding any loose materials, while those in the control plots were covered only partly with a light material of litter.

iv) Germination and /or natural regeneration conditions

After the treatment the experimental sites were fenced, and no other treatment of any sort was provided until the termination of the experiment, and was left to the mercy of nature and local biotic factors. However, during the second and last visit in

Figure 4.3: Photographs showing the 3 ground preparation treatments. Control (upper); Raking (middle), and Control burning (lower).

Figure 4.4: Photographs showing the view of the regeneration field experiment layout at Sanka-Meda, Arba-gugu forest.

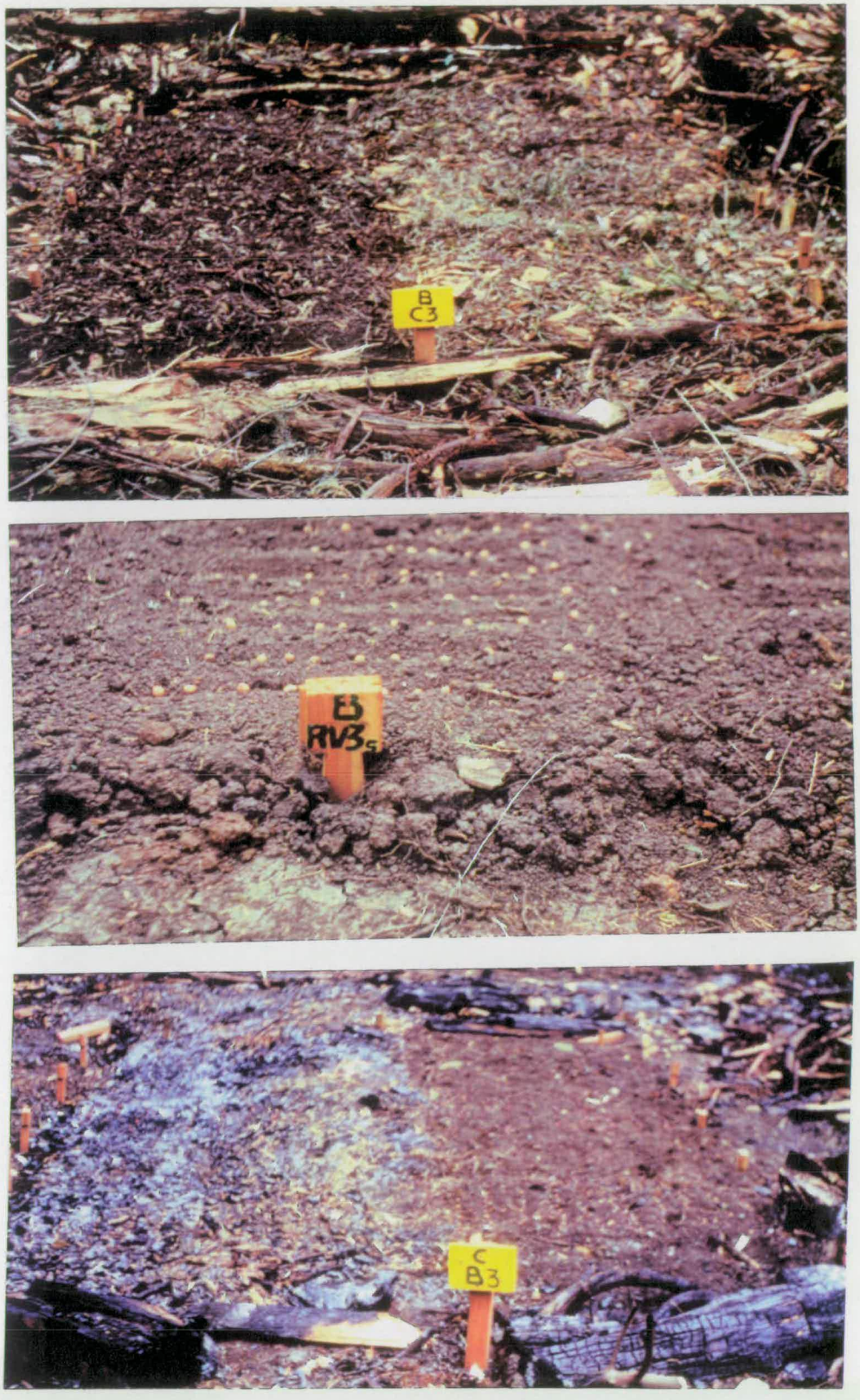

Fig. 4.5: Photographs showing the seedbeds and sown seeds. Control (upper); Raking (middle), and Control burning (lower). Note exposed *A. gracilior* seeds (middle).

December 1992, both experimental sites, at Sanka-Meda and Guna were found covered with a dense and over 1 m tall herbaceous weed growth of *Laggera tomentosa* Sch. Bip. (Asteraceae). The shade cover provided for different light levels was found removed. According to the local information, the shade cover of both sites and the fence at Guna site was removed by the local people on the first week of the experiment. Hence, the attempt made to get information on the effect of different levels of light for the whole duration of the experiment at the beginning of the experiment had failed. The fence at Sanka-Meda, however, was found intact. Generally, due to distance from villages and access road, the experimental site at Sanka-Meda experienced practically no disturbance, other than the removal of the shade-cover. The site at Guna, however, was under heavy pressure from cattle grazing and compaction due to its proximity to villages and access road.

4.3 Data collection and analysis

4.3.1 Natural regeneration microsites

Percentage PPF transmission of the regeneration sites was computed using the regression equation developed for the empirical model in Section 3.4.1. From the assessment of the regeneration sites the following variables were derived: number of seedlings of *J. procera*, *A. gracilior*, percentage PPF transmission, litter depth, percentage shrub, grass and forb cover. For a valid application of tests of significance in the analysis all data were transformed. Since seedlings were clumped and distribution was contagious log transformation was used for seedlings data. Arc sine transformation was used for all percentage data. The variation in each parameter was tested by Analysis of variance (ANOVA). Duncan's multiple range test was used to test the level of significance in the light environment between the sites. The effect of environmental variables at the plot level and the relationships between and within site was tested by analysis of covariance (ANCOVA) using SYSTAT statistical package. A general inspection of the distribution of residuals between and within site was made using a scatter diagram of the residuals plot.

4.3.2 Germination and/or natural regeneration data

Both experimental sites, Sanka-Meda and Guna were found covered with a dense and over 1 m tall herbaceous growth cover of *Laggera pterodonta* during the revisit in

December, 1992. Using the site plan, the experimental layout of all plots and sub-plots were identified and relocated. The *L. pterodonta* growth was carefully removed plot by plot from both experimental sites to facilitate data collection. At the same time, the PPF and the R:F-r ratios transmitted through the herbaceous weed cover and open were measured at about 10 cm above the ground level at Sanka-Meda experimental site.

The PPF was measured using calibrated quantum sensors and delta logger, Delta-T Devices, Cambridge, UK. The Red:Far-red ratios were measured using a Red:Far-red (SKR 110, Skye Instruments, Ltd Powys Wales, UK). The PPF sensors were monitored at 5-seconds intervals and the data logger recorded 30-min averages for 6 days.

After the removal of the weeds all seedlings germinated from sown seeds of both species were counted and their heights measured and recorded treatment by treatment. Naturally regenerated seedlings outside the sub-plots (unsown area) but within the experimental site were counted and recorded for each ground preparation. Information on the microsites of individual seedlings of natural regeneration and evidence of dispersal mechanisms were noted. The height and diameters at breast height (DBH) of trees within a width of 20 m around the edge of the clearing was measured to get an insight on the proportion and their size class distribution of the two conifer species, which might have contributed to the process of natural regeneration. A diameter tape and relascope were used to measure the DBH and the total height respectively.

From the raw quantitative data, the following variables were derived: number of natural regeneration, percentage germination and survival of sown seeds, height of seedlings germinated from sown seeds, height and DBH of trees at the edge of the clearing. Log and arcsine transformations were carried out for count and percentage data respectively. The variation in each parameter was explored by three-way analysis of variance (ANOVA). The level of significance in difference between the means of regeneration was tested using Duncan's multiple range test. Frequency distribution of height and DBH of all *J. procera* and *A. gracilior* trees around the edge of the clearing were calculated and histograms produced.

From the assessment of the natural regeneration microsite of each seedling over the whole experimental site qualitative information was obtained on the presence of bird

droppings with *J. procera* seeds, seedlings germinated on tree stumps, on fallen logs and the presence of current season young seedlings of less than two weeks.

4.4 Results

4.4.1 Microenvironment of natural regeneration microsites

i) PPF transmission

There was significant variation in percent PPF transmission among the regeneration sites (Fig. 4.6 and Table 4.1). Site 5, which was selected to be undisturbed control site, in fact was indistinguishable from the disturbed three sites (1-3) in terms of PPF transmission. The spatial variation in PPF transmission within each site differs from site to site. Photos taken at 2.5 m apart varied from a factor of 1.2 in most open site (4) to a factor of 24.6 in relatively closed canopy site (1) (Table 4.2).

Table 4.1: Summary of percentage canopy transmission of the natural regeneration sites. Means preceded by the same letter(s) are not significantly different from each other at $P \leq 0.05$ (F-statistics for one-way ANOVAS for variation among sites and Duncan's multiple range test). n = 16.

Site brief discription	Mean	Stdv	Min	Max
1. Burned 1974	c23.1	7.12	1.2	29.5
2. Dozer 1989	ba31.8	4.49	14.3	38.3
3. Burned 1972	bc25.5	8.24	5.3	38.3
4. Stripped and grazed	a49.5	0.55	43.8	54.5
5. Undisturbed	bc27.1	4.93	16.0	45.6
F-statistics (P-value)	22.19 (0.000)			

ii) Other microsite characteristics

There was no significant difference between the four disturbed regeneration sites in litter depth, while the undisturbed site (5) was significantly higher than the rest (Table 4.2). The litter depth in site 5 was about 7 fold that of the disturbed sites. There was a

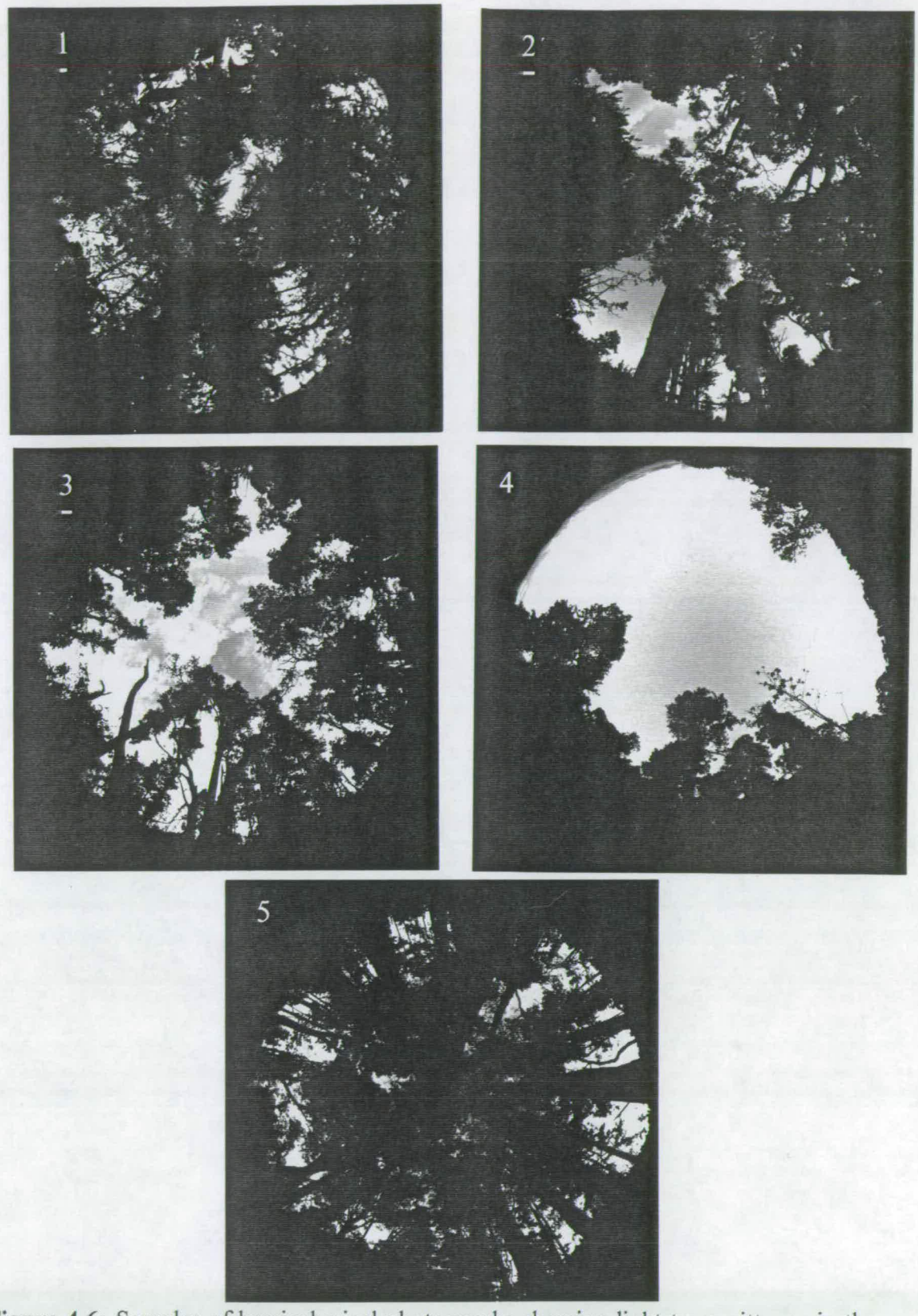

Figure 4.6: Samples of hemispherical photographs showing light transmittance in the forest floor of the regeneration sites. 1: Burnned 1974, 2: Dozer 1989, 3: Burned 1972, 4: Strippd and grazed, and 5: undisturbed control site.

significant difference both in grass and forbs cover between the sites. It must also be pointed out here, that the grass cover found in site 5 is not only the highest in terms of percentage cover, but also the tallest compared to the four disturbed sites. Sites (2 and 4) which were stripped off by dozzer are the most severely exposed microsites with the shortest vegetation cover. The most open site (4) had no shrub cover at all, while sites (1-3) did not differ significantly (Fig. 4.6; Table 4.2).

iii) Naturally occurring seedlings and microsite relationships

J. procera seedlings were found on all the four sites studied, while *A. gracilior* seedlings were found only on sites 1 and 3 disturbed by fire and absent in sites where the microsite was severely exposed by removal of the top soil. There was a highly significant difference ($F = 23.76$; $P < 0.001$) in number and distribution of *J. procera* seedlings among the four sites (Table 4.3). The most open site (4) had a significantly higher number of *J. procera* seedlings in all 16 plots than the other sites, while site 3 took the intermediate position both in number and distribution within the site.

Table 4.2: Characteristics of *J. procera* natural regeneration microsites following different disturbance history. Mean (±SE) of 16 plots of 2.5 m x 2.5 m each. Means preceded by the same letter(s) are not significantly different from each other at $P \leq 0.05$ (ANOVA and Duncan's multiple range test). Data are presented as original measurement.

Variable	Regeneration site					*F*	*P*
	Site 1	Site 2	Site 3	Site 4	Site 5		
Litter depth (mm)	b4.9 (0.53)	b3.9 (0.66)	b4.6 (0.43)	b4.3 (0.37)	a30.6 (2.18)	118.59	0.001
Grass cover (%)	b42.8 (2.92)	bc36.3 (4.44)	c30.3 (3.80)	c28.1 (3.09)	a54.7 (1.25)	10.694	0.001
Forbs cover (%)	c35.6 (3.19)	c34.4 (3.62)	b46.6 (5.06)	a59.1 (4.29)	bc41.9 (1.11)	7.30	0.001
Shrubs cover (%)	a16.9 (4.33)	a17.5 (3.38)	a14.7 (1.96)	b0.0 (0.00)	b4.1 (0.94)	4.49	0.006

Table 4.3: Number of *J. procera* and *A. gracilior* naturally regenerated seedlings in different microsites. Mean±SE of 16 plots of 2.5 m x 2.5 m each. Means preceded by the same letter(s) are not significantly different from each other at $P \leq 0.05$ (Duncan's multiple range test). Sites with no regeneration are excluded from the analysis.

Site brief description	Mean±SE
J. procera:	
1. Burned 1974	c1.0±0.33
2. Dozer 1989	c1.4±0.73
3. Burned 1972	b5.4±1.13
4. Stripped and grazed	a8.9±0.99
5. Undisturbed	0
A. gracilior:	
1. Burned 1974	1.6±0.53
2. Dozer 1989	0
3. Burned 1972	2.0±0.85
4. Stripped and grazed	0
5. Undisturbed	0

The distribution of seedlings in relation to PPF transmission litter depth, grass and forbs cover is illustrated in Fig. 4.7 and 4.8. Overall tests on the effect of microenvironmental variables on the number and distribution of both *J. procera* and *A. gracilior* seedlings of all sites using analysis of covariance reveals no association (Table 4.4). Examination of plots of residuals of all sites against all measured microenvironmental variables reveals no association. Also, there was no association between the size of the residuals and the estimated values.

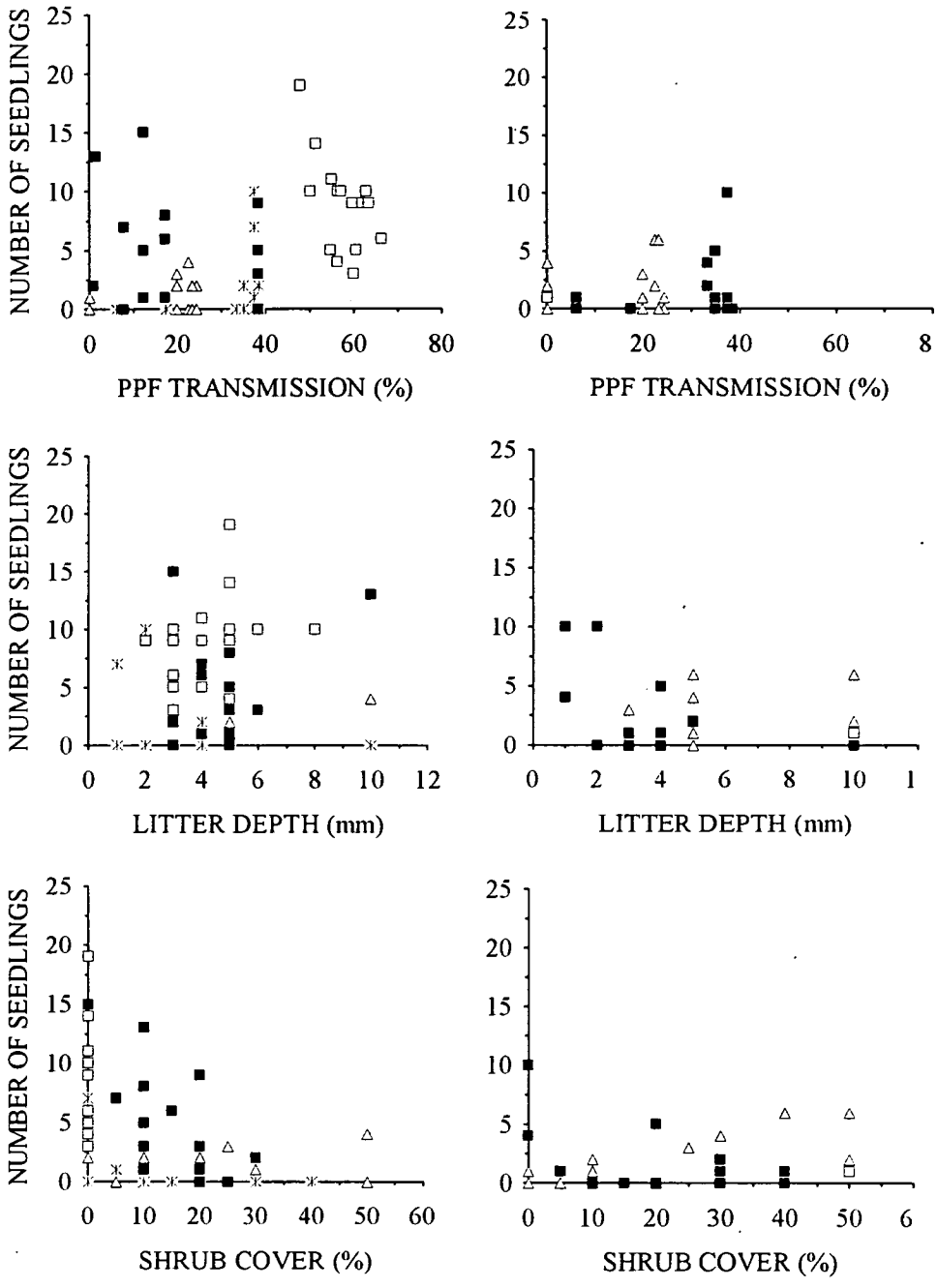

Figure 4.7: Number of *J. procera* (left) and *A. gracilior* (right) naturally regenerated seedlings in relation to percentage PPF transmission, litter depth and percentage shrub cover in four sites of different disturbance history in Arba-gugu forest. The data was collected from 100 m^2 each with 16 plots of 2.5 m x 2.5 m each from each site. Site 1: (△); site 2 (*) (*Juniperus* only); site 3 (▪), and site 4 (▫) (*Juniperus* only).

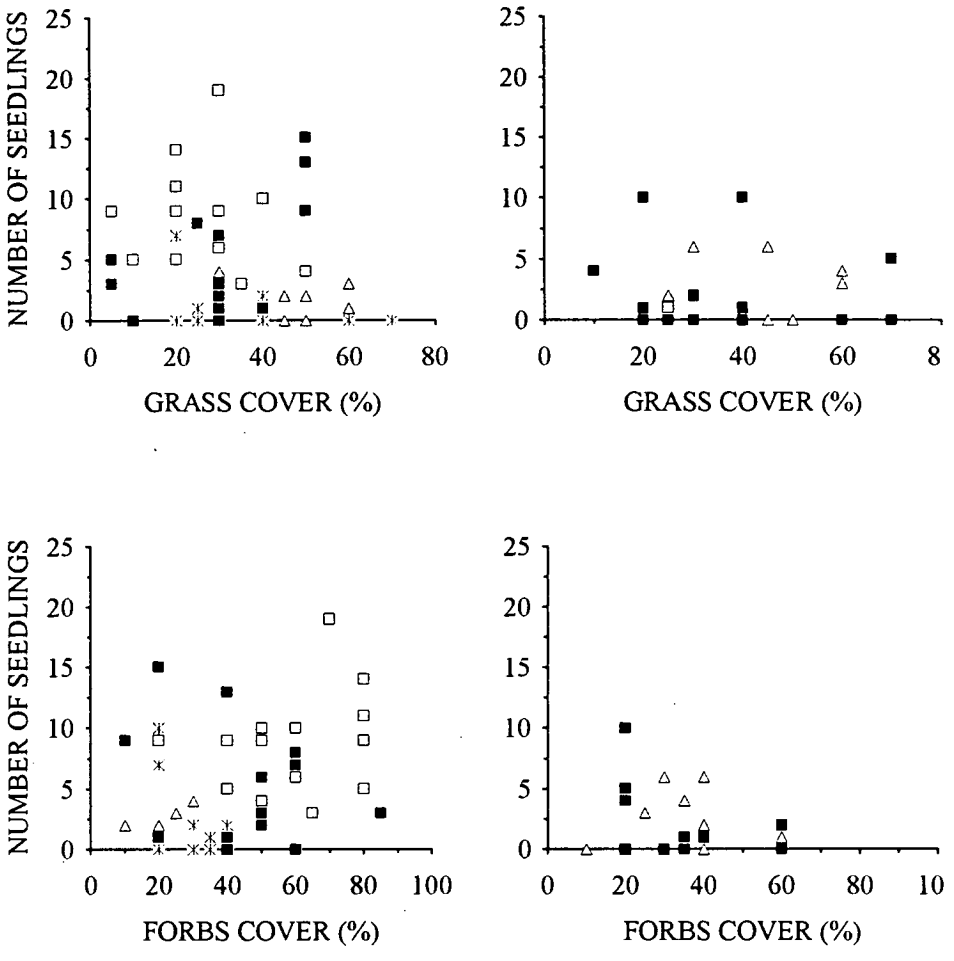

Figure 4.8: Number of *J. procera* (left) and *A. gracilior* (right) naturally regenerated seedlings in relation to percentage grass cover and percentage forbs cover. Site 1: (△); site 2 (*); site 3 (▪), and site 4 (▫). Other particulars are as described for Figure 4.7.

Table 4.4: Analysis of covariance (ANCOVA) for *J. procera* and *A. gracilior* natural regeneration distribution in relation to microsites. Naturally occurring seedlings as dependent variable and different factors as a covariate were tested for the presence of relationships.

Source	*Juniperus procera*			*Afrocarpus gracilior*		
	DF	*F*	*P*	DF	*F*	*P*
Site	3	12.616	0.000	1	0.113	0.740
Percent PPF transmission	1	0.536	0.467	1	0.001	0.974
Litter depth (cm)	1	0.472	0.495	1	0.010	0.921
Shrub cover (%)	1	1.455	0.233	1	1.904	0.180
Grass cover (%)	1	0.045	0.833	1	0.009	0.927
Forbs cover (%)	1	1.827	0.182	1	0.045	0.834
Error	55			25		
R^2		0.587			0.098	

Note: DF = degrees of freedom, *F* = variance ratio, and *P* = level of significance.

iv) Germination of soil seed bank

A total of 35 *J. procera* seedlings were recorded at the termination of the experiment after 10 months. The distribution of germinated seedlings between the samples were more or less even, in that all samples except one, had at least one seedlings. Nil, 1, 2, 3 and 4 seedlings were recorded in 1, 1, 10, 2 and 2 samples respectively. Germination started in week 3, the last seedling by about month 5 and no further germination took place thereafter until the termination of the experiment by month 10.

4.4.2 Effects of ground preparation on the germination and/or natural regeneration

Because of the heavy biotic disturbance experienced after the treatment by the Guna site and its poor result observed after the removal of the weed, it was found difficult to account the result to the treatment or to the disturbance. Also, due to the removal of the shade cover from both sites at beginning of the experiment, it seems impossible to provide information on the light environment experienced by the seeds and subsequently germinated seedlings for the whole duration of the experiment. Hence, no result on Guna site and no result on the light environment for the whole duration of the experiment will be reported in this study. The following results apply to the Sanka-Meda site only.

i) Light climate

Table 4.5 provides a comparative measure of the light conditions under the heavy weed growth of *Laggera pterodonta* in each treatment and open location from 6 days observations made just before the termination of the experiment during December 1992. PPF was significantly different among the three ground treatments. The percent PPF transmitted in the raking plots was 4 times greater than in the control plots. The burning plots took the intermediate position. The R:F-red ratio values under different treatments were clearly different from each other, decreasing with decreasing PPF, and were almost similar to those measured in the undisturbed part of the forest (Section 3.4.1). It must however be mentioned that a higher light level would be expected initially and during the dry season when the herbaceous weed growth drops its leaf.

Table 4.5: Descriptive statistics for the photosynthetic photon flux (PPF) and R:F-red ratios of the regeneration experimental plots under heavy growth of *Laggera pterodonta* (Asteraceae). Mean (±SE) 6 days observations. Both ANOVA and Duncan's multiple range test were conducted. Values with the same letter do not differ from each other significantly at $P \leq 0.05$.

Variables	Large clearing	Burning	Raking	Control
Percentage PPF transmission	100	b26.5±1.9	a55.6±2.8	c14.0±2.7
PPF (mol m^{-2} d^{-1})	24.8±3.4	b6.8±1.3	a13.9±2.2	c3.3±0.5
Range PPF (mol m^{-2} d^{-1})	15.0-35.2	3.1-11.0	7.7-21.3	1.7-5.1
Red:Far-red ratios	1.28±0.09	a0.65±0.06	a0.78±0.06	a0.53±0.05

ii) Artificial regeneration

There was a significant increase in percentage germination of *J. procera* seed with raking and burning ground preparation treatments on un-cultivated plots (Fig. 4.9; $P = 0.012$). The germination was high in the burning treatment and lowest in the control plots where all the logging waste and ground vegetation was left untouched. The raking plots took the intermediate position. The percentage germination was further increased with introduction of cultivation treatment. However, the effects of burning and raking were masked by cultivation giving a significant interaction in the full analysis but a non-significant main effect for ground preparation (Table 4.6. The

increase with cultivation was significant in the control and raking plots, while cultivation of the burning plots did not bring significant increase in germination.

The scenario of the effect of ground preparation on percentage germination became quite different when the germination of *A. gracilior* seeds were examined (Fig. 4.9). Percentage germination slightly increased with raking treatment, but decreased with burning treatment (Table 4.6). Moreover, the introduction of cultivation brought a further reduction on the germination of *A. gracilior* seeds (Table 4.6). Of the differences in percentage germination between the two species, germination of *J. procera* responded significantly to raking, burning and cultivation, while it was significantly lower in the control treatment than *A. gracilior* (Fig. 4.9).

The seedling height growth of both *J. procera* and *A. gracilior* were affected by ground preparation treatments (Table 4.6). Burning treatment brought a highly significant increase in the height growth of *J. procera* seedlings, while growth was significantly decreased in the raking treatment (Fig. 4.10). The seedling height of *A. gracilior* was significantly reduced with burning treatment, while there was practically no difference between the control and the raking treatment. The difference in height growth between the two species, *J. procera* seedlings height growth was significantly low in the raking treatment and significantly high in the burning treatment than *A. gracilior*, while the difference was negligible in the control treatment (Fig. 4.10).

Table 4.6: The effect of ground preparation (burning and raking) and cultivation on artificial regeneration (sown seeds)19 months after clear felling and timber extraction. Three-way ANOVA. (ns = not significant; *** P≤ 0.001; ** P≤0.01; * P≤0.05). (-) = less than control; (+) = more than control. See also Appendix 4.1.

	Probability				
Variables	Block	Plot	Ground preparation	Cultivation	Ground preparation * Cultivation
J. procera germination (%)	ns	ns	ns	+***	+**
A. gracilior germination (%)	ns	ns	ns	-*	ns
J. procera seedling height	ns	ns	+***	—	—
A. gracilior seedling height	ns	ns	-***	—	—

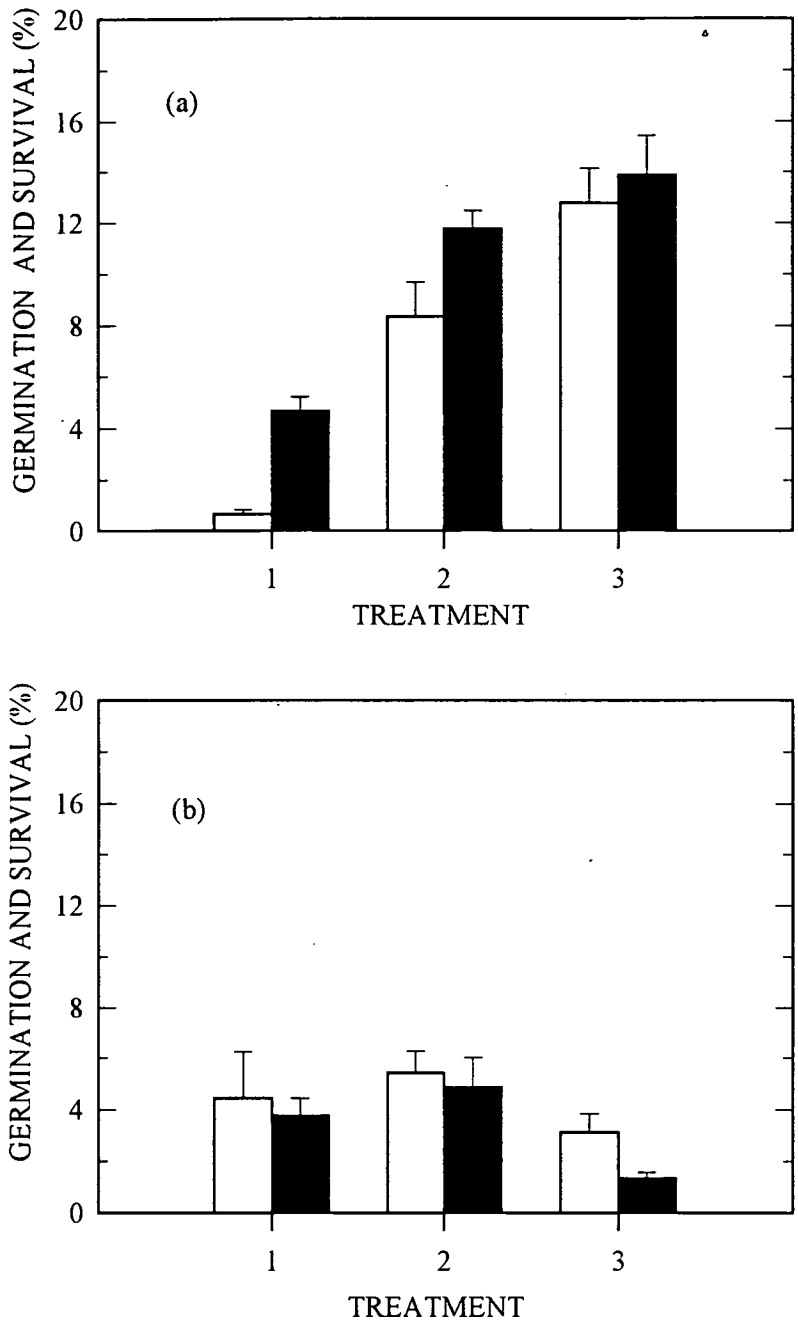

Figure 4.9: The effect of burning, raking and cultivation on the artificial regeneration of (a): *J. procera*; (b): *A. gracilior* 19 months after clear felling and timber extraction at Sanka-meda in Arba-gugu forest. 1: Control, 2: Raking, and 3: Burning. (▫) No cultivation and (▪) with cultivation. The layout of the trial plot and the details of the treatments are as described in the text. See also Appendix 4.2.

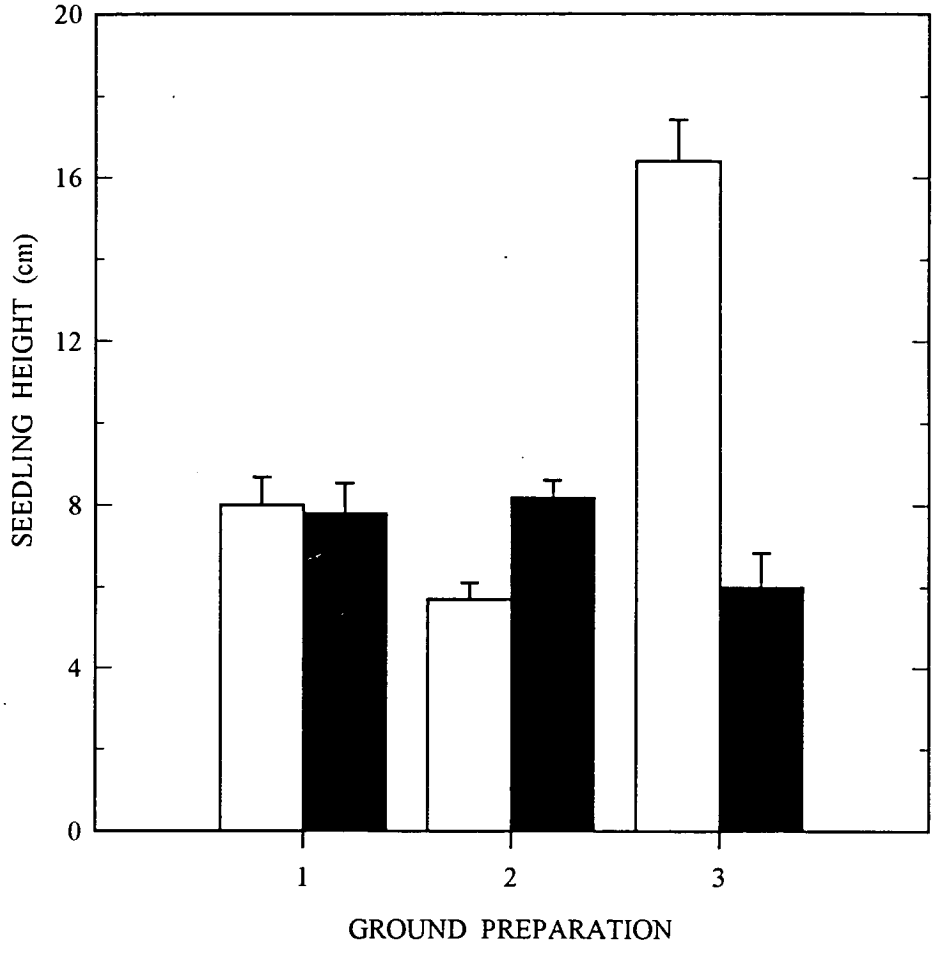

Figure 4.10: The effect of burning and raking (removal of all logging waste and ground vegetation) on the seedling height of sown *J. procera* (□) and *A. gracilior* (■) seeds 19 months after clear felling and timber extraction. 1: Control; 2: Raking and 3: Burning. See also Appendix 4.2.

iii) Natural regeneration

Ground preparation has a highly significant effect on the natural regeneration of *J. procera* ($F = 70$, $P = 0.001$, df = 8), while there was no sign of *A. gracilior* natural regeneration. Based on Duncan's multiple range test each treatment is significantly different from all others, at $P \leq 0.05$. Natural regeneration was at its peak in the burning treatment than both the control and raking treatments (Fig. 4.11).

From close examination of the experimental site in the natural regeneration zone during December 1992, about 25% of the naturally regenerated *J. procera* seedlings had germinated on tree stumps, and on and beside partially burned fallen logs in the raking and burning treatments, while none was found in the control treatment. Also, at several places within the experimental site, particularly in the burning and raking treatments several newly germinating seeds of *J. procera* were found in the fresh friut and from seeds in bird droppings. It is also clear from the height growth of the naturally regenerated seedlings compared to the sown seeds that seeds dispersed from 2 seed-years contributed to the natural regeneration.

It is also important to point out at this stage, that the higher germination both in artificial and natural regeneration did not occur in the treatment which experienced the highest light transmission (Table 4.5). The highest seed germination and height growth was in the burning treatment which had the intermediate light, while the raking treatment which had the highest light transmission was intermediate in germination and lowest in height growth. On the other hand, the control with the lowest light transmission was generally the lowest for *J. procera* germination and intermediate for *A. gracilior* germination. It is therefore clear from this that light does not seem to have any immediate effect on germination or height growth in this experiment.

To understand the process of natural regeneration in the undisturbed part of the forest and the source of seed supply, it is worthwhile to provide data on the proportion of trees of the two conifers size class distribution found in the immediate vicinity of the clearing while dealing with natural regeneration. Figure 4.12 illustrates the frequency distributions of height and diameter breast height (DBH) class of *J. procera* and *A. gracilior* trees found around the edge of the clearing. Both the height and diameter distribution of *A. gracilior* clearly demonstrate a positive and normal process of natural regeneration in the undisturbed part of the forest. On the other hand,

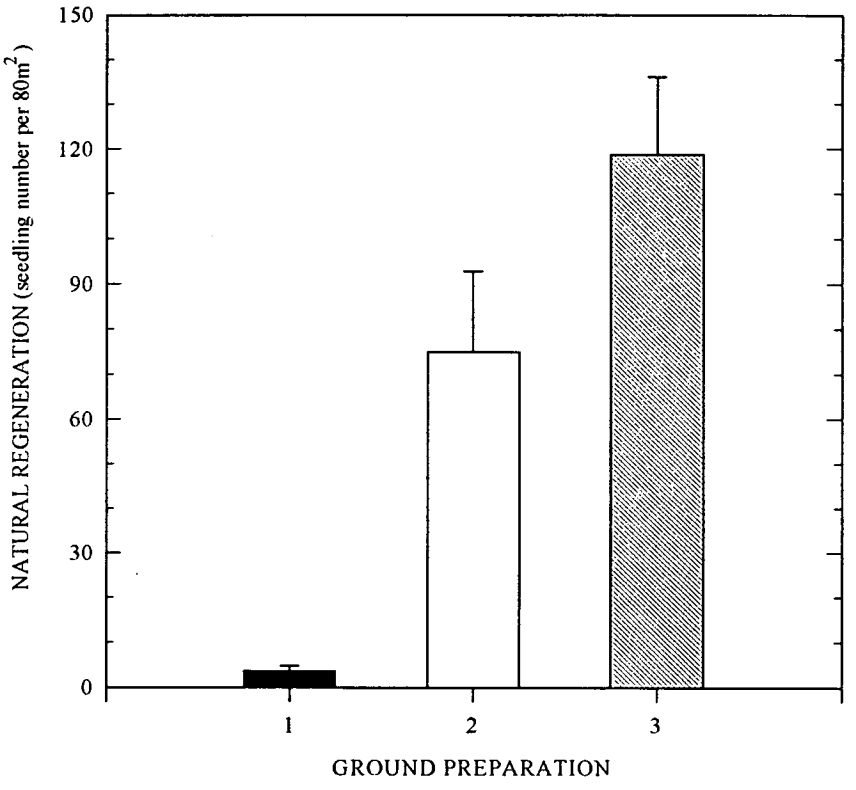

Figure 4.11: The effect of ground preparation on the natural regeneration of *J. procera* 19 months after clear felling and timber extraction at Sanka-Meda, Arba-gugu forest. 1: Control; 2: Raking, and 3: Burning. Mean number of seedlings over and area of 80 m^2. The error bar indicates the standard error of the mean. See also Appendix 4.2.

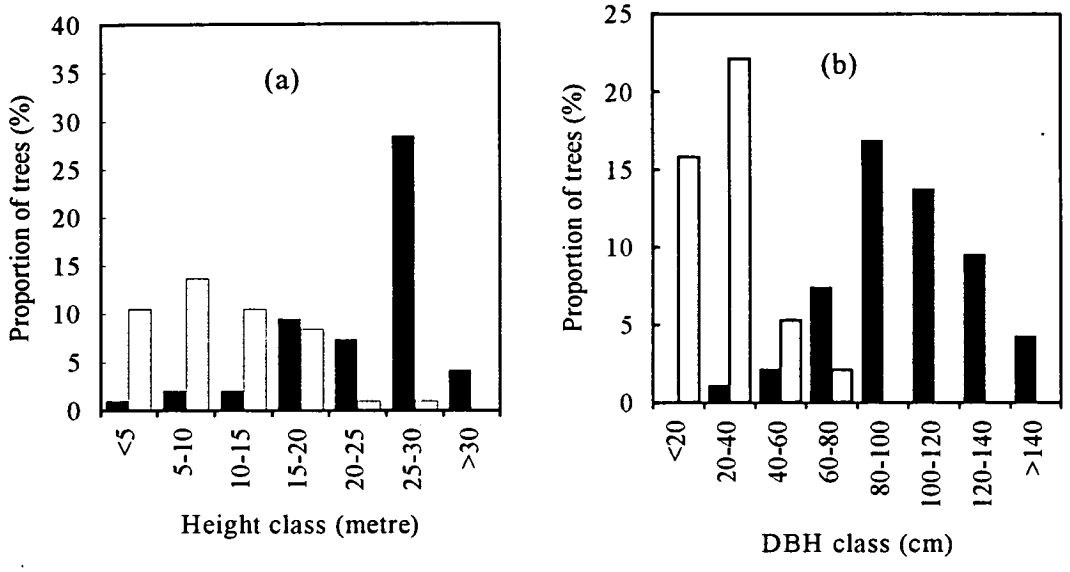

Figure 4.12: Frequency distribution of the proportion of height and diameter breast height (DBH) of *J. procera* (▪) and *A. gracilior* (▫) trees enumerated at the edge of the clearing 20 metres wide around regeneration experiment site at Saṇka-meda. (a): height class, and (b): DBH class distribution.

J. procera shows a high proportion of overmature trees and few specimens of younger trees. Overall, the proportion of *J. procera* to *A. gracilior* tree was 55% and 45% respectively. Of this only 11% of *J. procera* trees were under 80 cm dbh class and 44% greater than 80 cm dbh, while all *A. gracilior* trees were under 80 cm dbh class. When this is considered in terms of height class distribution, only 15% of *J. procera* trees were under 20 m and the rest above 20 m, while 43% of *A. gracilior* trees were under 20 m height class (Fig. 4.12). *J. procera* produces ripe seeds in that area during November and December yearly, while *A. gracilior* during February and March. At the time of the second visit *J. procera* was towards the end of seeding period.

Of the important information needing to be mentioned here, is the presence of *J. procera* seeds and new germinating seedlings embedded in fresh bird droppings. From field inspection of the forest stand around the experimental site several black winged love birds (*Agapovnis taranta*) were seen harbouring in the *J. procera* trees, while few were seen within the experimental site. Although detailed investigation was not carried out it is thought that this bird may play an important role in the process of natural regeneration being responsible for the seed dispersal and providing a pre-germination treatment.

4.5 Discussion

4.5.1 Microenvironment of regeneration microsites

Evaluation of the regeneration microsites demonstrated a lack of an overall association between the number and distribution of seedlings with light, litter depth, shrub, grass and forb cover in disturbed sites (Table 4.4). The lack of an overall association between the number and distribution of seedlings with light would not be surprising, since the level of light transmission was high in all sites. Studies conducted on the relationships between light intensity and regeneration indicate a negative relationship between regeneration and overstorey density for a number of species (Zeide, 1985). Fairbairn and Neustein (1970) also report greater germination in increasing light for a range of coniferous species and two-year greatest survival at 50% full light for some species. In contrast, other workers found far higher densities in areas of heaviest shade of the longest duration for some other species (e.g. McNeill and Thompson, 1982). Variations in the results of the above light studies probably

reflect the variation in response between species to light intensities. It is, however, to be understood that new plants can germinate and live within a tiny space of no more than a few centimetres in any dimension. What probably matters initially are the environmental conditions of these small microsites. Smith (1986) suggested that if microsite conditions are favourable, it makes no difference whether the spots are in the middle of a large clearing or a tree fall gap.

From field observation high numbers of young *A. gracilior* trees, saplings and seedlings are observed under pure *J. procera* and its own stands during field visits (see also Fig. 2.2 and Fig 2.10). Both species produce seed freely and they have abundant seeds in the soil and on the forest floor of both *J. procera* and *A. gracilior* stands. Yet, there are no signs of *J. procera* seedlings, while *A. gracilior* is freely regenerating beneath the *J. procera* trees. On the other hand, evidence of *J. procera* seedlings and saplings are found in locally disturbed soils, road-cuts and logging sites where the mineral soil is exposed (Fig. 2.11), and along compacted and abandoned trails. However, those seedlings which were found in several sites visited at Arba-gugu, Negele and Arero, were just as likely to have been in shade as in openings and no consistent pattern could be detected by casual observation. It is true that the amount of light reaching the soil surface is certainly greatly increased immediately after disturbance. However, considering the high light environment experienced in the *J. procera* and *A. gracilior* forest in this study (see Section 3.4.1), it is unlikely, that light is responsible for the lack of *J. procera* natural regeneration in the undisturbed part of the forest. Nevertheless, in order to test this hypothesis, it will be necessary to carry out glasshouse experiments in light regimes more nearly approximating those observed beneath natural vegetation, which may provide a basis for the differences in light requirement for germination of both species.

The litter depth may not affect the germination and subsequent seedling survival in all the disturbed regeneration sites in this observation, since the litter layer was very thin and there were no significant differences within and among sites. The shrub cover was very scattered, while the grass and the forb covers were short in all four disturbed sites, which all combined may have protected the germinated seedlings from other adverse effects. Moreover, seed germination can occur concurrently with litter fall, vegetation colonization, following disturbance by fire or removal of the vegetation which have exposed the mineral soil, the seedlings may have competed effectively in disturbed sites compared to the undisturbed site where an established cover would affect germination (McNeill and Thompson, 1982). Other workers suggest that

conditions suitable for germination are not those most efficacious for optimal development (McNeill, 1962), and regard a light vegetation cover of any species to be generally beneficial initially in the limitation of environmental extremes to which the young seedlings are particularly susceptible (e.g. Smith, 1986; Crawley, 1986).

4.5.2 Germination of the soil seedbank

This study clearly demonstrated that the soil seedbank of the forest floor in the undisturbed part of the forest contain viable *J. procera* seeds, which could have germinated if the ideal conditions had been met. Observation of the germination of seedlings from 16 soil seedbank samples scattered over an area of 100 m^2 resulted in a total of 35, indicating an average of 2.2 *J. procera* seedlings per sample. This represent not less than 9 viable seeds m^{-2}. Various factors regulate the germination of seeds in their natural habitat, some of which are internal, whereas others are external environmental factors (Mayer and Poljakoff-Mayber, 1989). Based on the microsite differences between the disturbed and undisturbed sites discussed above, the latter is considered to be the major factor for the inhibition of the germination of the viable seed of *J. procera* found in the seedbank in their natural environment. Various studies have reported the effect of vegetation on regeneration and the variation in microsite conditions brought about by different covers (McNeill, 1945; McNeill and Thompson, 1982). Grass is often reported to be very effective in preventing subsequent tree establishment (McNeil, 1955; Rehak, 1957; Dannatt and Davies, 1970; Robertson, 1976). Some grasses, once established, adversely affect either mechanically (Robertson, 1976) or by competing for moisture and nutrients and checking the young seedlings (Leyton, 1955). This is probably the reason for the lack of *J. procera* regeneration in the undisturbed part of the forest.

The adverse effect of thick forest floor litter in the undisturbed forest floor cannot be underestimated. Its effect probably is closely related with the moisture status of the microsite and preventing the seed and/or the young seedling to get in touch with the mineral soil. According to Smith (1986) forest floor litters generally lose water fast and are rarely hospitable to seedling roots. Large seeded species like *A. gracilior* may germinate more readily on thick litter than relatively small seeded species like *J. procera*. Carvell (1979) reports that the only species that can effectively establish themselves on thick leaf litter are those with large seeds (cited by Smith, 1986). However, this is not because they can germinate on top of such surfaces but because they were buried beneath the litter by rodents or more falling leaves and because

they have enough stored materials to grow back up through the litter. In contrast, most large seeds usually cannot successfully germinate on bare soil surfaces. Even if they do germinate, their new blunt roots simply roll them around over the surface without penetrating, and need to be buried to hold them in place and keep them moist for successful establishment. This view is further strengthened by Crawley (1986) who claims that seed and fruit morphology are amongst the most important determinants of microsite colonizing ability, in that the larger the seed, the less the disturbance necessary for successful establishment. He found vigorous seedlings of the big-seeded *Quercus robur* with their large acorns in the understorey of undisturbed site, where the small-seeded *Betula pendula* could not regenerate.

4.5.3 Effects of ground preparation on germination and/or natural regeneration

The field experiment conducted in this study, demonstrates convincingly the practical possibility of establishing *Juniperus procera* from seeds both artificially and naturally within a short time. It has been demonstrated that both burning of all logging waste *in situ* and raking (surface disturbance by scraping the litter and mor humus following removal of all logging waste and ground vegetation) increased germination of sown seeds and natural regeneration when compared with undisturbed controls. Comparing the two treatments, the burning gave a higher percentage germination compared to the raking. Moreover, cultivation of the burning, raking and the undisturbed control plots further improved the germination. Successful germination of seed and establishment of seedlings on bare mineral soil seedbed has been reported by different workers for various species. A recent review by Fowells and Means (1990) provides the findings of other workers, who recommend exposure of the mineral soil by burning or mechanical scarification to create an appropriate environmental conditions for natural or artificial regeneration for *Pinus palustris, Juniperus occidentalis, Pinus echinata, Larix occidentalis, Pinus taeda Pinus virginiana*. Such seedbed preparation reduced the number of *Pinus taeda* seeds required to produce one seedling (Fowells, and Means 1990). They found that, undisturbed seedbeds with a litter depth of 8 to 10 cm required 5 to 6 times more seeds to produce the number of seedlings produced in disturbed seedbed. Post-fire increased seedlings establishment in *Cistus salvifolia* has also been related to litter removal, and that the burning of litters at the soil surface could eliminate some germination inhibitors derived from leaching and/or litter decomposition (Went, 1952). Other studies also revealed similar results for

Engelmann spruce and Norway spruce (Noble and Alexander, 1977; Meshechok, 1956). Tree litters accumulating in large quantities and persisting for years in temperate and boreal forests have a direct effect on vegetation, in contrast to the warm moist conditions of tropical forests where leaves are known to disappear in few months (Packham and Harding, 1982). So is the case with *J. procera* and *A. gracilior* coniferous forests compared to the broadleaved forests particularly those found in more humid and wetter parts of the Country. Unincorporated organic matter such as litter and other plant remains that lie on the mineral soil does not make a good seedbed for most small-seeded species unless disturbed (Smith, 1986). There is a positive relationship between the roughness of the surface and the proportion of various species germinating; that is increasing germination for small-seeded species with increasing disturbance (Harper *et al.*, 1965).

Disappointingly, no natural regeneration of *A. gracilior* was found, and germination of sown seeds was very low under all condition. Rather a decreasing tendency in germination with increasing disturbance was demonstrated; that is germination in the burning treatment was low, with further decrease with cultivation. The obvious explanation for this result is that most large seeds usually cannot successfully germinate on bare soil surfaces (e.g. Smith, 1986); this, however, do not explain for the absence of germination on the cultivation treatment where the seeds were covered.

Because of the ideal weather condition, higher moisture content of the fuel and its uniform distribution over the plot, except where the bigger stemwood contributed to some patchiness of the fire, the treatment achieved the intended objective resulting in a good regeneration. Many authors emphasize the importance of the moisture content of the fuel and its even distribution over the area to be treated, the season and the weather condition during fire treatment for control burning (review by Hare, 1961; Brown, 1974; Norum, 1977; Perry and Lotan, 1977; Debyle, 1981).

More pertinent to the discussion of natural regeneration, however, is the quantity of ripe seed supply, dispersal mechanisms and the distance to which the seed, sufficient enough to establish the site, can be expected to arrive (e.g. Smith, 1986; Hart, 1991). Moreover, regeneration and its distribution pattern is also influenced by the distribution of seeds around each parent tree (Packham and Harding 1982, Fenner 1987). Both *J. procera* and *A. gracilior* produce fleshy fruits (berries) and drop their seeds almost vertically. Seeds are disseminated by birds and fruit eating

mammals such as black winged love birds (*Agapovnis taranta*), colobus monkey and baboons found in the forest. Animals ingest the fruit but do not digest the seeds. Dissemination of seeds by animals is evidenced by seed-filled droppings, particularly black winged love birds for *J. procera* and columbus monkey and baboons for *A. gracilior*. *J. procera*, however, seems to have an advantage over *A. gracilior* due to its smaller size seed which are ingested and easily dispersed to the experimental site by the black winged love bird as evidenced perched birds. While *A. gracilior* seeds are mainly ingested by colobus monkey and baboons, which mainly sit trees and deposit their droppings within the undisturbed part of the forest and rarely visit the experimental site in the large clearing, where there are no trees in which to sit. This is probably the main reasons for lack of sign of *A. gracilior* seeds passed through the digestive tract of the animals feeding on them, while it is widespread in the forest. Therefore, the lack of natural regeneration of *A. gracilior* at least in the control plots, despite very little disturbance during logging and one seed-year during February and March, is probably partly attributable to clear felling system without leaving some scattered seed-trees within the experimental site for animals to perch and dessiminate the seed with their droppings.

Available information generally supports the result obtained about *A. gracilior* in this study, in that those species that germinate significantly better in the forest understorey than in the large clearing are not found in highly disturbed areas or other high light environments (Crawley, 1986). For instance, lowland dipterocarp forest may regenerate either in the forest understorey or in forest gaps, but they are not typical components of early successional or highly disturbed areas such as those described by Kochummen (1966), Kochummen and Ng (1977), Wyatt-Smith (1949, 1955). It can therefore be predicted from this, that *A. gracilior* which does germinate better in the undisturbed forest understorey does not germinate well in the large clearing and particularly in the highly disturbed site .

The result further demonstrated an increased height growth with burning treatment and a decreased growth with raking treatment compared to control for *J. procera*, while *A. gracilior* was indifferent with raking and control with a significant decrease in burning treatment. The implication of this result for *J. procera* seems very clear. The height growth of *J. procera* in the raking treatment may have been reduced due to the complete removal of the nutrient rich materials such as the leaves, twigs, rootlets, bark, and especially the litter layers of the forest (e.g. Binkley, 1986; Smith, 1986; Matson, *et al.*, 1987). Although in early growth, nutrient supply may not

present much of a problem for survival, other workers found similar results on degraded soils, where nitrogen and mineral deficiency restricting growth, with enhanced condition when in competition with ground vegetation (McNeill, 1955). In contrast, the increased growth of *J. procera* seedlings in the burning treatment must have been a result of the added nutrient due to burning. This is because most of the nutrient elements that are of essentially mineral origin stored in logging waste are returned the soil in more readily available form after burning than before harvest, improving the chemical properties of the soil (Smith 1986). Simth (1986), however, suggest that faster height growth of a species than its competitors at an early stage is a criterion of a species adaptiblity capacity to clear cutting, whilst species that grow slowly in juvenile stages, even if planted, are those shade-tolerant species which are not well suited to clear cutting system. This means that *J. procera* is probably more exposure-tolerant and responsive to nutrient supply compared to *A. gracilior* at an early stage.

Based on data collected both on height and diameter distribution in the immediate vicinity of the clearing, *A. gracilior* clearly demonstrates a positive and normal process of natural regeneration in the undisturbed part of the forest. On the other hand, *J. procera* has a high proportion of overmature trees and few specimens of younger trees. Similar results were reported by other workers on the process and trend of natural regeneration for the same forest (Chaffey, 1979; Ungethüm and Jordan (1990).

4.6 Conclusion

Finally, based on artificial and natural regeneration after 19 months of the experiment, and on the observed microenvironment phenomena of the natural regeneration microsites and the soil seedbank, it may be concluded that:

1. Light transmission reaching the forest floor of the undisturbed part of the forest was indistinguishable from that in some of the disturbed natural regeneration microsites, suggesting that light may not be the main factor for lack of regeneration of *J. procera*.

2. Despite the presence of viable seedbank in the undisturbed forest floor, removal of the overstorey vegetation by clear felling did not encourage natural regeneration of *J. procera*.

3. Germination of sown seeds and natural regeneration of *J. procera* was significantly better on disturbed soils where the mineral soils are exposed by burning and mechanical scarification. This clearly suggests the importance of manipulating the ground vegetation rather than canopy trees for the natural regeneration of *J. procera*.

4. Clear felling or ground preparation either by burning or mechanical treatment did not result in the natural regeneration of *A. gracilior*.

5. Exposure of the mineral soil by mechanical scarification did not improve germination of sown seed of *A. gracilior*, while exposure by burning inhibited the germination.

6. The black winged love birds (*Agapovnis taranta*) are the agents mainly responsible for the dispersal of *J. procera* seeds, while colobus monkey and baboons, and other endemic mammals may be responsible for *A. gracilior* seed dispersal.

7. Ground preparation by burning significantly improved height growth of *J. procera* germinated seedlings, while those of *A. gracilior* were significantly decreased.

8. Finally, it may be said that *J. procera* is capable of enduring exposure, and its natural regeneration is compatible with 'clear cutting with seeding from adjacent stands' together with ground treatment, particularly controlled burning which exposes the mineral soil. In contrast, both the regeneration felling method and the ground treatments employed in this study, will discourage the natural (or artificial) regeneration of *A. gracilior* suggesting that *J. procera* is a pioneer species which is more exposure-tolerant, whilst *A. gracilior* is more shade-tolerant and exposure-intolerant.

On the basis of the limited amount of light data presented in this chapter, however, it may be unwise to attempt to predict the effect of light on germination and/or seedling

growth. It seems necessary therefore, to carry out investigations in which simulated canopy light is an experimental variable, in an attempt to understand the influence of shade upon the seed germination and seedling growth of *J. procera* and *A. gracilior* in a more controlled environment in the following chapters.

CHAPTER 5

Effects of Pre-germination treatments and Simulated Canopy Light on Seed Germination: A Glasshouse Experiment

5.1 Introduction

Both *Juniperus procera* and *Afrocarpus gracilior* have a low percentage of germination under natural conditions. Although Gardner (1926) claimed that *J. procera* is a strong light demander which does not regenerate where there is any organic material covering, the light requirement of both species for germination has never been well documented. Pre-germination treatments for *J. procera* are controversial. For example, Laurant and Chamshama (1987) found a significantly high germination with hot water and H_2SO_4 pre-germination seed treatment and no germination for untreated seeds. In contrast, Jones (1989) and Negussie, *et al.* (1991) reported no significant effect on such pre-germination seed treatments over the control.

In the preceding Chapter it was demonstrated that the viable soil seedbank of *J. procera* which remained dormant under the unaltered forest canopy, germinated when spread on a germination tray in a glasshouse. While opening of the canopy by removing the overstorey did not result in good natural regeneration or germination of sown seeds, exposure of the mineral soil by mechanical scarification and fire treatment resulted in good natural (or artificial) regeneration. On the other hand *A. gracilior*, which regenerates better in the undisturbed part of the forest, did not show a positive response under all treatments under field conditions. The specific variables responsible for differences in germination, particularly of the sown seeds cannot be deduced from field study alone. It seems necessary, therefore, to carry out investigations in which light intensity and quality are experimental variables, in an attempt to understand the influence of shade upon the germination of *J. procera* and *A. gracilior* seeds.

The purpose of this Chapter is to explore the effect of pre-germination treatments and different level of light on the seed germination of *J. procera* and *A. gracilior*. Factors that promote or inhibit germination of *J. procera* and *A. gracilior* are investigated. The study comprised two glasshouse experiments: (a) effects of various pre-

germination treatments on percentage and speed of seed germination, where effects of chitting, cutting tips of seed coat, heat shock, hot water and acid treatments (HCl and H_2SO_4) were examined; (b) effects of photon flux density on percentage and speed of seed germination, where high, medium, low and dark treatments with varying Red:Far-red ratios were tested.

5.2 Material and methods

5.2.1 Experimental material

Seeds of *J. procera* collected in August 1992 from Menagesha forest (37°45'E - 38°25'E and 9°0'N - 9°15'N) in central Ethiopia were received from the Forestry Research Centre, Ethiopia, in early September 1992. Seeds of *A. gracilior* collected in March, 1992 from Arba-Gugu forest in south-east Ethiopia were used. The seeds had a purity of about 90 and 100% respectively. The seeds were separated in water by floating off empty seeds. About 50% of *J. procera* and 98% of *A. gracilior* total seed was retrieved and thoroughly rinsed in tap water to remove any sticky exudates. They were then dried at room temperature for 48 h and stored in a cold room at temperature of about 5 °C for a week. A considerable proportion of the floating *J. procera* seeds had insect holes and deep surface wrinkles. Some of the *J. procera* seeds which sank also had insect holes, which suggested they were not viable. *A. gracilior* seeds were stored under the same conditions for 6 months before the treatment.

Sound *J. procera* seeds of similar size with minimal surface wrinkles were carefully separated out from the sunken seed in an attempt to maintain maximum uniformity of seed quality. For the viability of the embryo 100 seeds of each species were tested with 2% concentrated tetrazolium chloride for 24 h (ISTA, 1985) and viability was found to be 57% and 100% for *J. procera* and *A. gracilior* respectively.

5.2.2 Treatments and experimental design

Two experiments involving a total of six seed pre-germination treatments and four light treatments were carried out in a glasshouse for 20 weeks between 23/09/92 and 21/02/93. In each experiment, a completely randomized block design with five replications was adopted. In each treatment 100 seeds were used for each species.

The pre-germination experiment on *J. procera* and *A. gracilior* involved the following treatments before imbibition:

1. Control: no treatment.

2. Chitting: rubbing the surface of seeds with sand paper so as to improve conditions for moisture penetration.

3. Cutting the tips of seed coat at one end and provide an inlet for moisture.

4. Heat-shock treatment by placing dry seeds in an oven at 100 ^{o}C for 2 minutes.

5. Immersing seed in a beaker containing 200 ml of concentrated hydrochloric acid (HCl) stirred for 15 min. The seeds were then washed and rinsed in distilled water.

6. Immersing seeds in a beaker containing 200 ml of concentrated sulphuric acid (H_2SO_4) and stirred for 15 min. Seeds were then washed and rinsed in distilled water.

7. Immersing seeds in 100 ^{o}C boiling water for 1 min then cold distilled water and cool to room temperature.

The light experiment involved high, medium, low and zero light treatments. To obtain a range of shade each pot was provided an individual 'shade-cover'. For the cover one layer of 430 clear filter, chromid 211ND filter, blue green filter and aluminium foil were used for high, medium, low and dark treatments respectively (Table 5.1). The shade-covers for high, medium and low treatments were fixed at the top of the pot with masking tape, while the dark treatment pots were wrapped with aluminium foil to totally exclude light. The clear filter cover used for the high light treatment was intended to maintain a similar microclimate within all treatments. Although no attempt was made to separate light levels from light quality in this experiment, due care was taken to ensure that the simulated shade was characterised by reduced photosynthetic photon flux (PPF) and low Red:Far-red ratios.

In each experimental unit 20 seeds were planted with the radicle (tapered end) in down germination pots filled with pure sand. Each pot constituted a plot in a

randomised block design. A single replicate of each of the six treatments and 1 control for the pre-germination experiment and the four treatments for the light experiment were set-up in each germination tray and each tray constituted a block. Five germination trays for each experiment were placed on an experimental bench in a glasshouse.

Table 5.1: The filter materials used for the 'shade-cover' and their light environment during the germination of *J. procera* and *A. gracilior* seeds in a glasshouse. Mean±SE.

Filter materials used	PPF ±SE (mol m^{-2} d^{-1})	Percent PPF transmission	R/FR ratio (±SE)
Open experimental bench	9.1±0.5	100	1.07±0.06
1 layer 430 clear filter	8.3±0.4	91±4.6	1.07±0.07
1 layer 211ND filter	2.0±0.1	22±4.2	0.29±0.03
1 layer blue green filter	0.3±0.01	3±0.3	0.08± 0.005

The criterion for germination was when the radicle, hypoctyl and cotyledons were well visible. All except the dark treatment were inspected weekly for germination. Germinated seeds were counted, recorded and discarded. The germination of the dark treatment was not recorded until the termination of the experiment. At termination of experiments, ungerminated seeds were subjected to the tetrazolium chloride test of viability.

5.2.3 Germination conditions

After three days on the experimental bench the germination trays of the pre-germination treatments were covered with a white polythene sheet to maintain moisture and warmth. In each experiment, the pots were kept moist through seepage from the germination trays. Water was added in to the germination trays as and when necessary.

The photosynthetic photon flux (PPF) of the light experiment outside and inside each shade-cover on the experimental bench was measured for two weeks continuously, using calibrated quantum sensors and delta logger, Delta-T devices RS 232, Delta-T Co. Ltd Cambridge, UK. The Red:Far-red ratios were measured using SKR 110,

Skye Instrument, Ltd., Powys Wales, UK. This enabled definition of the light level inside the shade-covers as 91%, 22% and 3% in relation to the open experimental bench. Red:Far-red ratios of 1.07, 1.07, 0.29 and 0.08 were recorded for open bench, clear filter, 211ND filter and blue green filters respectively.
Although air temperatures were partially controlled in the glasshouse, the temperatures on the experimental bench were highly variable, ranging from 13.7 to 24 °C during night and 21.1 to 33.2 °C during day.

5.3 Data collection and analysis

At the end of 20 weeks, germination was expressed as percent of all seeds sown and the mean calculated. After arc sine transformation of the percentage figures, the data were subjected to analysis of variance (ANOVA). The level of significance in differences between treatment means was guaged by Duncan's multiple range test. Treatments which produced very low percentage germination figures were excluded from the analysis.

5.4 Results

5.4.1 Effects of seed pre-germination treatment on germination

Pre-germination seed treatment with H_2SO_4 and hot water of both *J. procera* and *A. gracilior* and heat shock treatment of *A. gracilior* seeds resulted in nil germination. Germination of *J. procera* seeds was significantly reduced in heat shock and HCl acid pre-germination treatments, while cutting did not significantly increase germination over the control, and chitting treatment took the intermediate position (Table 5.2). Germination of *A. gracilior* seeds was significantly increased in the cutting pre-germination treatment, whilst germination was lower but not significantly in chitting and HCl acid treatments than the control.

Figure 5.1 provides full information on the germination time course of both species based on accumulated percentage germination against time. Speed of germination of *J. procera* varied slightly between pre-germination treatments. The cutting and chitting treatments started germination in the first week of the treatment and produced 33% and 20% germination respectively in 3 weeks time. The heat shock treatment,

gave faster germination rate than the HCl acid treatment, but had no beneficial effect over the control. Germination in the cutting and chitting pre-germination treatments and in the control reached the maximum in week 9 and 10, while HCl and heat shock pre-germination delayed until week 17 and no further seed was germinated till week 20.

Table 5.2: Effect of different pre-germination treatments on final percentage seed germination of *J. procera* and *A. gracilior* 20 weeks after sowing. Mean (±SE). Analysis of variance (ANOVA) and Duncan's multiple range test were conducted on the arc sine transformed data. Values followed by the same letter do not differ significantly from each other at $P \leq 0.05$. Data are reported as original percentage germination. (*) Treatments which resulted in nil germination were excluded from the analysis. For all tests, d.f. = 4. See also Appendix 5.1,

Variable	Control	Cutting	Chitting	HCl	Heat shock	Variance ratio (F)	Level of significance
J. procera	a32 (2)	a39 (3)	b29 (3)	c21 (2)	c21 (3)	6.97	0.002
A. gracilior	b15 (2)	a60 (5)	b14 (1)	b11 (1)	0* (0)	57.52	0.000

Germination rate of *A. gracilior* varied greatly between pre-germination treatments (Fig 5.1). The cutting treatment had a much greater beneficial effect over the control and all other treatments. The cutting treatment started with 4% germination in the third week, reached a maximum rate of 34% in the fourth week, the final 60% germination by week 8 and no germination was seen thereafter till the experiment was terminated by week 20. The chitting treatment completed germination by week 11, while the HCl acid treatment had no beneficial effect over the control. Both HCl and control reach their peak by week 8 and showed very slow germination rate thereafter until germination was completed by week 15.

Comparing the germination of the two species, *J. procera* had a much higher final percentage and a faster germination rate than *A. gracilior* under all conditions, with the exception of cutting pre-germination treatment where *A. gracilior* showed a much higher percentage germination.

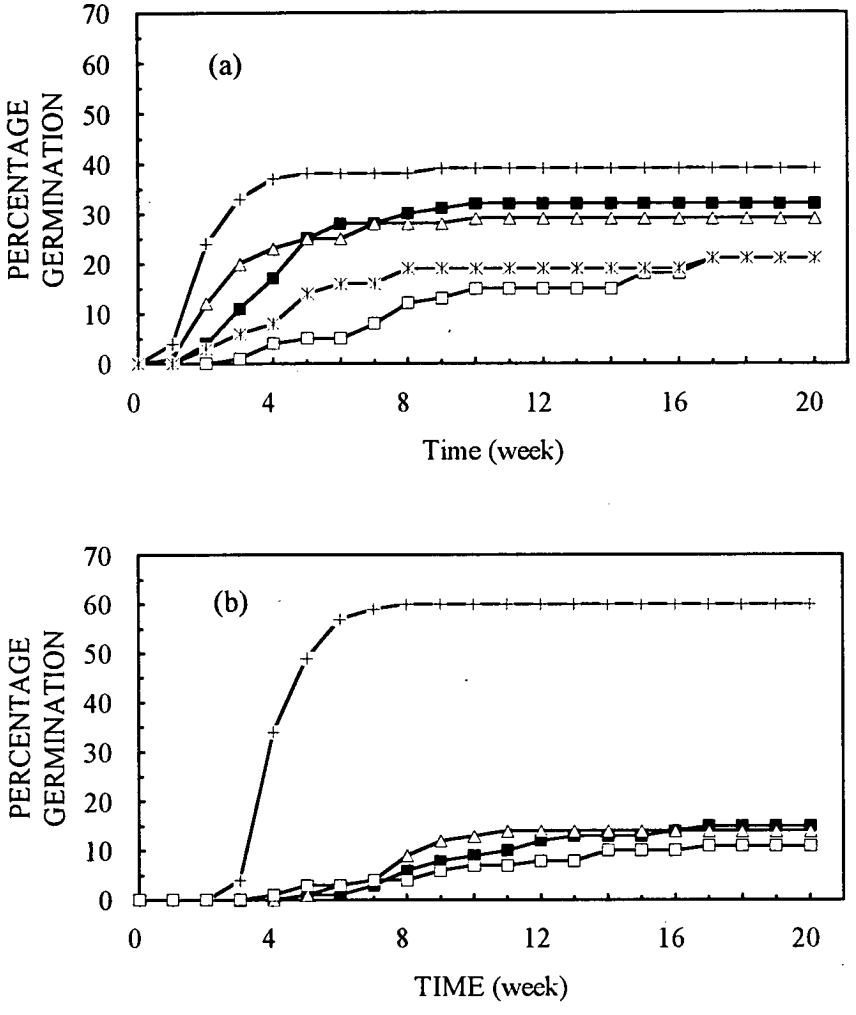

Figure 5.1: Time-course of seed germination of *J. procera* (a) and *A. gracilior* (b) after different pre-germination treatments. Control (▪); chitting (△); cutting (+); HCl (▫) and heat shock (*). The details of the treatment and other germination conditions are as described in the text.

At the termination of the experiment after 20 weeks, a test of the ungerminated *J. procera* seeds for embryo viability demonstrated that all seeds were dead. *A. gracilior* seeds used in control and chitting pre-germination treatment showed about 50% and 45% viability respectively, while those seeds used in other pre-germination treatments were found not viable.

5.4.2 Effects of light on seed germination

The effect of different photon flux densities with varying R:F-red ratios on the germination of seeds of both species including dark treatment and simulated canopies are presented in Table 5.3 and Fig. 5.2. Both species reached maximum germination in the dark treatment, with an increasing trend from high light to dark treatments. However, the increase in percentage germination of *J. procera* seed was not significant between treatments, while the increase in *A. gracilior* seeds was significant between treatments (Table 5.3). In *A. gracilior* an inhibition was recorded in the high light treatment.

Table 5.3: Final percentage germination of *J. procera A. gracilior* seeds under varying photon flux densities and varying R:F-red ratios 20 weeks after sowing. Analysis of variance (ANOVA) and Duncan's multiple range test was conducted on the arc sine transformed data. Values followed by the same letter do not differ significantly from each other at $P \leq 0.05$. Standard error values are given in parentheses. For all tests, d.f. = 4. Data are reported as original percentage germination. See also Appendix 5.1.

Variable	Light levels				Variance ratio (F)	Level of significance
	High	Medium	Low	Dark		
J. procera	a27	a30	a32	a34	0.74	0.546
	(3)	(2)	(5)	(3)		
A. gracilior	c20	b38	ab45	a54	8.84	0.002
	(4)	(8)	(8)	(4)		

There were differences between treatments in the time-course of germination under simulated canopies on both species (Fig. 5.2). *J. procera* showed a faster germination rate compared to *A. gracilior*, in that it started germination earlier and completed earlier than *A. gracilior* in both experiments. The seedlings of both species germinated in the dark treatment were etiolated; that is they were very long and pale.

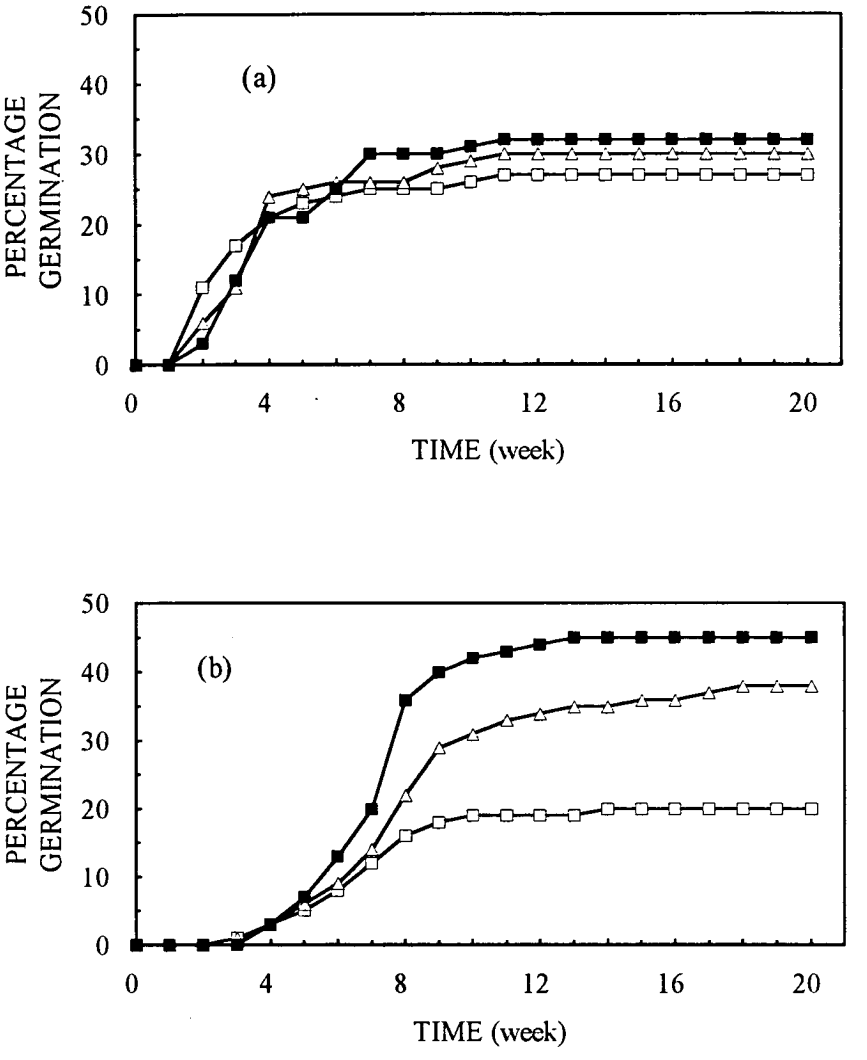

Figure 5.2: Time-course of seed germination of *Juniperus procera* (a) and *Afrocarpus gracilior* (b) under simulated canopy with varying light intensity and R:F-red ratios. High (□); medium (△) and low (▪) light treatments. The details of the treatment and other germination conditions are as described in the text.

Viability test of the ungerminated seeds at the termination of the experiment showed that seeds of both species in the dark treatment were found non-viable, while seeds in simulated canopies had viabilities averaging 10% for *J. procera* and 25% for *A. gracilior*.

5.5 Discussion

5.5.1 Effects of pre-germination treatments

J. procera seeds used in this study germinated with no treatment, or following some mechanical or chemical scarification pre-germination treatments. The results of this study, conflict with a study conducted in Tanzania (Laurent and Chamshama, 1987), where immersing in hot water for 30 and 60 sec and soaking in H_2SO_4 for 5, 10, 20 and 30 min pre-germination treatments resulted in 68 to 74% and 70 to 78% germination respectively in the first 14 days, while in the present study, germination was nil over the 20 week period with 60 sec hot water and 15 min H_2SO_4 pre-germination treatments.

Moreover, Laurent and Chamshama (1987) failed to germinate untreated *J. procera* seeds, while 32% germination was recorded for the untreated seeds in this study. Jones (1989) for *J. procera* seeds collected from Eritrea, found only 35% germination after 240 days with 30 min H_2SO_4 pre-germination treatment, and significantly lower germination for 60 min acid scarification. Also Negussie *et al.* (1991), for seeds collected from Kenya, found 5% germination after 18 weeks with 10 min H_2SO_4 pre-germination treatment, and even lower for 20 min H_2SO_4 pre-germination treatment.

The obvious differences which may explain the discrepancies in results between his study and that of Laurent and Chamshama (1987) is the duration of the experiment. Considering the 85% viabilities obtained at the termination of their experiments, the short experimental period of 14 days may not have permitted the untreated seeds to germinate. These inconsistencies suggest that different seeds with possibly different physiological and collection histories may respond differently to the same germination conditions (e.g. Daniel *et al.*, 1979). The results obtained in this study, however, are similar to those of Jones (1989) and Negussie *et al.* (1991) who recorded germination over a longer period (about 33 and 18 weeks respectively) after sowing, and found

that pre-germination treatments did not result in a significant beneficial effect over the control.

The lower seed germination percent for the heat shock pre-germination treatments of *J. procera* seeds than the control and lack of germination for *A. gracilior* in this experiment indicate that fire *per se* probably does not stimulate the seed germination of these species. Fire, however, creates improved seedbed conditions for the germination of *J. procera* by exposing bare mineral soils and suppression of potential competitors (Section 4.5.2; see also Hall, 1984). The result obtained in this experiment contrasts with the findings of Laurent and Chamshama (1987), where they found increasing germination (50 to 60%) by fire-scorching with grass half to thrice the weight of the seed and no germination for the control in their Tanzanian experiment. In the current experiment, heat shock at 100 ^{o}C for 2 minutes decreased germination from 32% for the control to only 21% for the heat shock treatment. Analysis of Keeley's (1987) data on 45 Californian shrubs shows that all the species with heat-stimulated germination produced dry fruits, mainly exploding capsules, while species with heat-inhibted germination had either fleshy or dry fruits. Similarly, a study by Mazzoleni (1989) in the Mediterranean demonstrated a relation between fruit type and germination behaviour of seed to heat treatment. *Cistus monspeliensis* and *C. incanus* which produce dry capsules, show a significant increase in germination with increasing heat treatment from 80 to 160 ^{o}C and time of exposure from 30 to 120 seconds, while *Arbutus unedo* and *Myrtus communis* which have fleshy fruit showed decreased germination with increasing temperature and time of exposure.

The explanation for the differences between the result of this experiment and that of Laurent and Chamshama (1987) is difficult. Although temperature may increase with increasing the layer of grass used in the fire-scorching treatment, in the absence of such information as the actual temperature at which the seed was heated and the time of exposure to that unknown temperature, it is impossible to provide an appropriate explanation for the difference. Hence, the results obtained in the above studies agrees with the findings in this study, in that germination of *J. procera* and *A. gracilior* which produce fleshy fruit cannot be heat-stimulated and such treatment would inhibit their germination. Moreover, the lack of total germination of *A. gracilior* at similar temperature treatment with *J. procera* probably confirms that it is more susceptible to heat than the latter.

The lack of seed germination in hot water pre-germination in this study, agrees with the results of Jones (1989) and Negussie *et al.*, (1991) where they found that hot water pre-germination completely inhibited *J. procera* seed germination. In other studies, it was found that dry seeds of several species withstood 110 ^{o}C for 4 hours, in water, soft seeds were killed in 5 minutes at 60 ^{o}C to 82 ^{o}C which suggests that heat resistance of seeds is inversely correlated with moisture content (review by Hare, 1961). Thus, the hot water seed pre-germination treatment of 100 ^{o}C for 2 minutes in this study was lethal to *J. procera* and *A. gracilior* seed.

The results of the present study clearly demonstrated that mechanical scarification by removal of the seed coat at the radical end was the best pre-germination seed treatment for the germination of both species, particularly to *A. gracilior* seeds. However, sulphuric acid, which is widely known to improve germination of seeds that have hard seed coats (FAO, 1985) appears to result in no germination. Moreover, soaking the seed in concentrated HCl and chitting pre-germination treatments did not result in improved germination in this study. These results agree with other studies conducted by Chamhama and Downs (1982) and Munyarugerero (1983), who found 81% and 70% germination respectively by complete removal of seed coat and no germination by soaking the seed in H_2SO_4. Only the inner seed coat seemed responsible for controlling the germination of *A. gracilior* since removal of the outer layer (pericarp) alone in the control did not activate germination, while cutting the tip of the seed coat to increase in water permeability increased percentage germination from 15% to 60%. Most hard-coated seeds, in nature become permeable to water when the seed coat is broken down by passage through the digestive tract of animals causing it to crack (e.g. Mayer and Poljakoff-Mayber, 1989). Similarly, it is probably the birds and wild animals such as Colobus monkey and baboons, which feed on the seed of *A. gracilior* and *J. procera* are responsible for the natural regeneration success in the natural environment, by making the seeds more permeable to water when the seed coat passes through their digestive tract (Chapter 4). Despite repeated claims in the literature, however, that seed coat dormancy can be broken by mechanical abrasion or chemical softening of the seed coat, this study has failed to demonstrate this.

5.5.2 Effects of light treatments on germination

The results of this study demonstrate convincingly that the seeds of *J. procera* and *A. gracilior* can germinate under all conditions of light. The species have shown a

similar trend by increasing germination with decreasing light levels. However, germination of *A. gracilior* seeds becomes significantly higher at low light levels. Although the control of seed germination by light has been a subject of countless investigations (Grime and Jarvis, 1975), there are no studies conducted on the light requirements of these species for seed germination to compare with the results of this study. However, the response observed in the present study is closely similar to other studies conducted by Kinzel (1926) who found those categories of species which are indifferent to the presence or absence of light (cited by Mayer and Poljakoff-Mayber, 1989).

It is apparent from the results that maximum germination of *A. gracilior* is reached in the dark treatment, a feature which is consistent with the very high proportion of *A. gracilior* regeneration in the understorey of the undisturbed forest floor observed in the field. It is interesting to note, however, that the seeds of *J. procera* which do not appear to germinate in the understorey of the undisturbed forest floor and mostly colonize open bare ground, reached the highest percentage germination in complete darkness in this study. This probably indicates that, in natural environments, factors other than light intensity and spectral composition intervene as major determinants of the location, timing and success of germination of *J. procera*.

5.6 Conclusion

Based on 20 weeks germination test period it may be concluded that:

1. Despite the low viability (57%) the percentage germination of *J. procera* was good compared to some of the previous published works.

2. A range of pre-germination treatments failed to significantly improve the percentage germination of *J. procera*.

3. Of the range of pre-germination treatments, conducted only cutting the seed coat at the radical end significantly improved the percentage germination of *A. gracilior*.

4. Sulphuric acid and hot water pre-germination treatments resulted in nil germination for both species.

5. Heat pre-germination treatment decreased germination in *J. procera*, while totally inhibited germination of *A. gracilior*.

6. *J. procera* seed germination showed indifferent behaviour to the presence or absence of light, while dark treatment significantly improved percentage germination of *A. gracilior*.

CHAPTER 6

Response of Seedlings to Light Regime and Nutrient Supply: A Glasshouse Experiment

6.1 Introduction

In Chapter one, the response of species to light and nutrient supply was reviewed. It was also pointed out in Chapter four that *J. procera* showed a more exposure-tolerant behaviour in the field and a strong response to nutrient supply in the seedbed compared to *A. gracilior*. Hence, in this Chapter, an attempt will be made to confirm the results obtained under field conditions in a more controlled environment regime of light and nutrient regime.

The objective of this experiment was to investigate the response of *J. procera* and *A. gracilior* seedlings to shadelight and nutrient supply under simulated light conditions of understorey habitat, clearings and disturbance gaps. This was achieved by growing seedlings in a glasshouse under simulated forest shade by artificially reducing photosynthetic photon flux (PPF) and red:far-red (R:F-r) ratios under low and high nutrient levels. No attempt was made to separate PPF from light quality. The experiment was conducted between 24 March and 22 August 1992 (20 weeks).

6.2 Material and Methods

6.2.1 Plant material and experimental design

Seeds of *J. procèra* and *A. gracilior* were sown in germination trays containing equal parts by volume of vermiculite and perlite. The seedlings were potted into 21-cm long and 6.5-cm diameter plastic tubes filled with equal volumes of vermiculite and perlite. The seedlings' age at the start of the experiment was 2-3 weeks and the height ranged from 2.4 to 4.5 cm for *J. procera* and 3.8 to 7.0 cm for *A. gracilior*. Plants were

sorted into 10 blocks of 8 plants of similar height to minimize the within-group variance.

Eight treatments were applied to the eight seedlings in each block in a randomised block design with 10 replications were set up on an experimental bench in the glasshouse for growth analysis. The treatments include: four PPFs (i) deep shade, (ii) low, (iii) medium and (iv) high light intensities, and two nutrient levels (i) low and (ii) high, giving 8 treatments in all. Due to the small amount of plant matter expected, an additional set of samples with 5 seedlings of *J. procera* was set up for leaf anatomy and leaf chlorophyll content determination.

6.2.2 Design and light regime of 'shade-covers'

Each plant was provided with an individual 'shade-cover' using a 7.5 cm diameter and 24.0 cm long plastic tube, cut at both ends, covered with Strand filters (Northern Light, Edinburgh) fixed at the distal end with masking tape. The outer part of the tube was covered with aluminium foil to avoid transmitted light. See Fig. 6.1 for the shade-cover construction, and Fig. 6.2 for the layout of the experiment. The objective of the filter design was to simulate forest shade by reducing photosynthetic photon flux (PPF) and red:far-red (R:F-r) ratios (Kamaluddin, 1991).

The advantage of individual shade covers is that each plant is independent of all the others, thus avoiding the problem of pseudoreplication that arises when large enclosures are utilized.

The light transmission and spectrum of the filters were scanned using a spectroradiometer (model 6000, Monolite Instruments Ltd., Surrey, UK) comprising a system controller (68010 OSA module, 6830 HeNe module, 6841 Interface Card-IBM At., 6850 Std. software 200-1500 nm), scanning monochrometer 6162, tungsten halogen light source with IR filter 6130, integrating sphere 6118 and PMT unit 6771+6173A.

To simulate and obtain a range of shade, two layers of chromid 211 plus one layer of chromid 209 for deep shade; one layer chromid 211 0.9 N.D, filter for low light, and

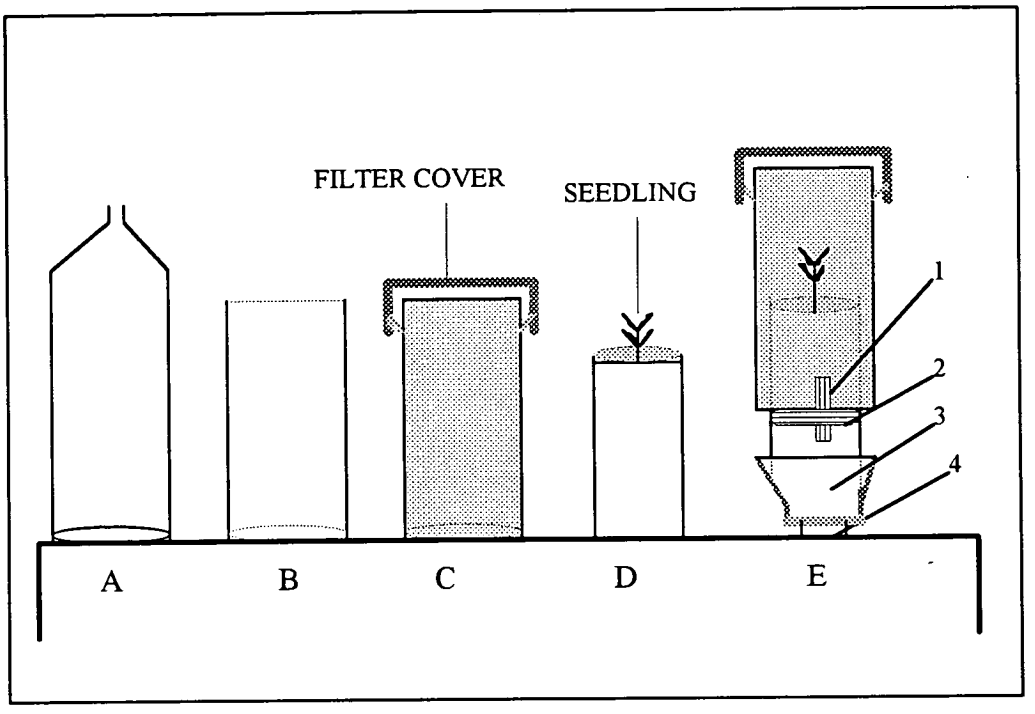

Figure 6.1: Diagrammatic representation of the 'shade-cover' construction used for growing *J. procera* and *A. gracilior* seedlings in a glasshouse. A: a plastic container; B: the container cut at both ends into a tube; C: the tube covered with aluminium foil with a filter cover on the top; D: a growth tube filled with equal volumes of vermiculite and perlite mix, with a seedling transplanted into it; E: the shade-cover supported by sticker (1) fixed on to the growth tube by adhesive (2), the growth tube standing in a pot (3) on a petri-dish (4).

Figure 6.2: Photograph showing the layout of the experiment on an experimental bench in a glasshouse. Seedlings under 'shade-cover': (left and right sides). Measurement of environments (light, wet- and dry-bulb air temperature) on the open bench and under different light treatments connected to delta-logger for data acquisition: (centre).

one layer of chromid 209 plus one layer of plastic netting for medium light treatment were used. To maintain a similar micro-climate inside the tubes the 'open' high light treatment was also provided with one layer of clear filter no. 430.

The PPF was measured using a quantum sensor (Li-190 SB Li-Cor Inc., Lincoln, USA). Initially, the PPF outside and inside each 'shade-cover' on the experimental bench was recorded for two weeks continuously, using 5 calibrated quantum sensors and delta logger, Delta-T Devices Ltd, Cambridge, UK. Measurements were taken every 5 min, and stored as 1-hour averages on the data logger. This enabled definition of the PPF inside the shade covers at the start of the experiment. The light levels inside the clear filter was 90% of the open. The light levels inside the shade-cover were 4%, 20%, and 40% in relation to the clear filter, for deep shade, low and medium light treatments respectively. The light both on the experimental bench and inside 'shade-covers' was recorded for the duration of the experiment.

The R:F-r ratios were measured using a Red:Far-red sensor SKR 110, Skye Instruments, Ltd., Powys, Wales, UK. The R:F-r ratios were measured throughout the day at hourly intervals and the mean ratio for each treatment was calculated from 12 readings.

6.2.3 Temperature and humidity

To determine the differences in air temperatures and humidity, 'dry-bulb' and 'wet-bulb' temperatures outside and inside the shade-cover on the experimental bench were sampled at 5 minutes interval and recorded as hourly averages for two weeks. Thermocouples (Copper-constantan thermocouple wire, British standard BIO BS 1843 Type T.T.C. Ltd. Uxbridge, UK), 24 AWG, and the Delta-logger were used to record dry-bulb temperatures (T_a) and 'wet-bulb' temperatures (T_w). An air temperature shield was provided at the junction to reduce radiation errors on the thermocouples. The junction of the thermocouple used for the wet-bulb was inserted in to a wet wick immersed into a small bottle filled with de-ionized water to keep it moist. Both dry-bulb and wet-bulb thermocouple wires were fixed on to the inner wall of the seedling pot within the shade-cove'. The other end of the two wires for both dry- and wet-bulb were connected to the Delta logger for data-acquisition.

The vapour pressure deficit (δe) was calculated as:

$$\delta e = e_s(T_a) - e$$

where $e_s(T_a)$ = saturation vapour pressure (kPa) at T_a, and e = actual vapour pressure (kPa) given by:

$$e = e_s(Tw) - \gamma (T_a - T_w)$$

where $e_s(T_w)$ = saturation vapour pressure (kPa) at T_w, and γ = psychometric 'constant', taken as 0.08 kPa $°C^{-1}$ for the unaspirated 'wet-bulb'. The values for $e_s(T_a)$ and $es(T_w)$ were obtained from Sandford's (1982) Table.

Air temperature and relative humidity/vapour pressure deficit in the high light treatment was recorded for the duration of the experiment. Due to the very high temperature encountered in the glasshouse during May the south-western part of the glasshouse was painted white to lower the temperature until the termination of the experiment.

6.2.4 Nutrition

The seedlings were fed with a nutrient solution modified from Ingestad's solution (Ingestad, 1979). Solution 'B' was modified to exclude nitrogen, potassium and phosphorus salts so as to allow the application of the same level of minor and trace elements for all treatments. The levels of the other elements were raised to maintain the ionic balance as in the original solution B. The composition of the final stock nutrient is shown in Table 6.1.

Two litres of each solution ('A' and 'B') were made and kept in separate bottles until making up appropriate solutions and mixed in a large volume of de-ionised water.

Solution A and B were diluted in the ratio of 0.9:1 and 0.03:1 with de-ionised water to provide 30 and 1 mg l^{-1} of N for high and low nutrient levels respectively. The aim was to provide all roots with this standard solution daily. Nutrient solution was, therefore, applied once a day as irrigation until it began to flow from the drainage hole, to bring the medium to field capacity. The transfer of nutrients from one treatment to another on the experimental bench was protected by mounting each

seedling pot on a petri-dish.

The position of each seedling with similar nutrient treatments within the same block on the experimental bench were exchanged daily so as to share any differences in incoming light that may exist. Also, the shade cover of similar light treatments within a block were exchanged to share the differences that may exist in the construction. The level of the shade-covers were raised upwards progressively as the seedlings increase in height.

Table 6.1 The composition of the final stock nutrient Ingestad's solution used to feed the seedlings in the glasshouse.

Solution 'A' ($g\ l^{-1}$)		Solution 'B' ($g\ l^{-1}$)	
Composition	quantity	Composition	quantity
$NH_4\ NO_3$	140.2	H_2SO_4	1.470
KNO_3	37.2	H_3BO_3	0.570
KH^2PO_4	41.3	$FeC_6H_5O_7.5H_2O$	4.190
K^2SO_4	14.0	$(CH_3COO)_2Ca$	13.790
		$(CH_3COO)_2Mg4H_2O$	37.530
		$MnSO_4$	0.550
		$CuCl_2$	0.032
		$ZnSO_4$	0.036
		$NaMoO_4$	0.007

6.3 Data collection and analyses

6.3.1 Growth data

Ten additional seedlings representing the whole range of plants at the start of the experiment were harvested initially (t_1) for destructive measurements. After measuring leaf area (A) the samples were dried in an oven at 100 ^oC for 24 hours and leaves, stem and roots were recorded. The height of seedlings and number of leaves of

the seedlings were recorded weekly during the experiment period.

Finally, after 20 weeks of growth (t_2), remaining plants were harvested and total height, hypocotyl length, number of leaves and leaflets of the 80 seedlings were recorded. Leaf area in cm^2 was measured using the leaf area meter (LI-1300 Li-Cor, Lincoln, USA) and leaves were oven dried in the same manner as the initial harvest (t_1) for dry weight determination.

Mean relative biomass growth rate (R), stem extension growth rate, and net assimilation rate (E), were calculated in the period t_1 to t_2. Leaf area ratio (F), specific leaf area (S), leaf weight ratio (w), specific stem length (L), stem weight ratio (s), root weight ratio (r) were determined at final harvest (t_2).

Mean relative growth rate was found as described by Evans (1972) and Hunt (1978) were used for the growth analysis:

$$R = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

R is growth rate in dry weight (W) per unit time (t). Where, W_1 = total plant dry weight at t_1, W_2 = total plant dry weight at t_2 and ln = natural logarithm.

$$E = \frac{W_2 - W_1}{t_2 - t_1} \cdot \frac{\ln A_2 - \ln A_1}{A_2 - A_1}$$

E, net assimilation rate, is the rate of increase in dry weight per unit leaf area, per unit time, and is an estimate of the carbon assimilatory capacity of leaves A_1 = leaf area at t_1 and A_2 = leaf area at t_2. This equation assumes A is linearly related to W (Hunt 1978). Linear regression between plant dry weight and leaf area indicates that they were indeed highly and positively correlated (*J. procera*: $r = 0.93$, $n = 60$, $P \leq 0.001$; *A. gracilior*: $r = 0.82$, $n = 60$, $P \leq 0.001$).

$$F = \frac{A}{W}$$

F, leaf area ratio, is the ratio of leaf area (A) to total plant dry weight (W) and represents the ratio of photosynthesising to respiring material within the plant (Hunt 1982).

$$w = \frac{W_L}{W}$$

w, leaf weight ratio, is the ratio of leaf weight (W_L) to total plant dry weight (W). It is a dimensionless index of the leafiness of the plant on weight basis.

$$S = \frac{A}{W_L}$$

S, specific leaf area, is the mean area of leaf (A) displayed per unit of leaf dry weight (W_L) and is a measure of leaf density or relative thickness (Hunt, 1982).

Thus, it is clear from the above equations that:

$$R = E \,.\, F; \text{ and } F = S \,.\, w$$

S is more often sensitive to environmental changes and more prone to ontogenic drift than W, and thus a change in F should be reflected in S or w.

$$s = \frac{W_S}{W}$$

s, stem weight ratio, is the ratio of stem dry weight (W_S) to total plant dry weight (W).

$$L = \frac{L_S}{W_S}$$

L, specific stem length, is the mean length of stem (L_S) displayed per unit of stem dry weight (W_S).

$$r = \frac{W_r}{W}$$

r, root weight ratio, is the ratio of root dry weight (W_r) to total dry weight (W).

Also, weekly stem extension rate and stem growth over time was calculated. The same biomass growth rate formulae were used to calculate stem extension rate. Root length of each sample was also measured.

6.3.2 Leaf anatomy

Before the final harvest and after 18 weeks of growth, leaf anatomy data were collected, including stomatal density, thickness of leaf, palisade tissue and spongy mesophyll.

A surface replica impression was made on both leaf surfaces using silicone rubber and transparent varnish for the determination of stomatal density. The stomatal densities were counted using a calibrated grid in the eyepiece of a light microscope covering a microscopic field of 1 mm^2 on 5 seedling samples.

For the determination of leaf thickness, palisade tissue, and spongy mesophyll a transverse section of the leaf blade sample was prepared. Leaf samples were taken from the mid height of the seedling at mid point of the leaf blade from 5 seedlings for each treatment. The sample was prepared using an embedding medium for frozen tissue specimens and an MSE Freezing Microtone slicer, which uses liquid CO_2 for freezing the sample. The transverse section was then measured using a graticule under the light microscope.

6.3.3 Extraction and determination of leaf chlorophyll content

Leaf chlorophyll contents were determined from two sets of 5 to 6 mature leaves of *J. procera* and 2 to 4 mature leaves of *A. gracilior*. Pair of leaves of the same size were taken from opposite sides of the stem at the mid-point of each seedling on 5 samples for each treatment. Leaf area of half of each sample was measured and c. 2.5 cm^2 of one set of leaf material was put in an oven for 24 hours at 100 ^oC for

dry weight determination. The second samples of c. 2.5 cm^2 was extracted using N.N' -dimethylformamide (DMF) following the method described by Porra, *et al.*, (1989). The sample was immersed in 3 ml of the solvent DMF and kept in the dark for 24 hours to extract the chlorophyll for determination.

The leaf chlorophyll contents were determined using a spectrophotometer (SP800, Unicam, Sweden) at 647 and 664 nm. Concentrations of chlorophylls *a* and *b* were calculated from the absorbance value using the following equations of Ziegler and Egle (1965) cited by Šesták (1971). These are in (mg l^{-1}):

Chlorophyll *a* = $11.78a_{664} - 2.29a_{647}$

Chlorophyll *b* = $20.05a_{647} - 4.77a_{664}$

Chlorophyll (*a*+*b*) = $7.01a_{664} + 17.76a_{647}$

Where, a_{664} is the absorbance at 664 nm wavelength.

6.3.4 Determination of leaf nitrogen content

The leaf nitrogen contents of both *J. procera* and *A. gracilior* of each treatment were determined from the dry leaves of all samples. After the determination of the dry weight the leaves of each sample were ground separately in a Mixer mill (Glen Creston, Stanmore, England). The percentage nitrogen content of each sample was determined using a Flow Injection Analyser (Tecator Fiastar 5020, supplied by Perstorp Analytical, Thornbury, Bristol).

6.4 Statistical analysis of the data

The variation in each parameter was investigated by analysis of variance (ANOVA) using the statistical package Minitab. For the purpose of locating significant differences between treatments, Duncan's new multiple-range test (DNMRT) was used (Steel and Torrie, 1960).

6.5 Results

6.5.1 Microclimate

(i) Light

The clear-filter had a transmittance that is more or less constant at all wavelengths between 400 nm and 800 nm, while chromid 209 and 211 had a low transmittance in the red (660 nm) relative to the far-red (730 nm) (Fig. 6.3a). The spectral distribution of light under the clear-filter was slightly higher at the red relative to far-red, while the 211 filter was significantly deficient in the red and blue, as is vegetational shadelight. The 209 filter was also lower in the red and blue relative to far-red and took the intermediate position (Fig. 6.3b).

Fig. 6.4a illustrates the diurnal pattern of photosynthetic photon flux (PPF) under each treatment. The total daily pattern of PPF for the duration of the experiment in the different light treatments is presented in Fig. 6.5. The mean total daily PPF was generally low ranging from 0.35 in the deep-shade treatment to 9.01 mol m^{-2} d^{-1} in the high light treatment (Table 6.2). The PPF level was lower for the first four weeks of the experiment, and increased gradually. There was a slight decline in PPF at the beginning of May in the glasshouse compared to outside due to the white paint applied to the glasshouse. However, the desired range of shade was achieved and the R:F-r ratios were not affected as the paint was optically neutral (Table 6.2). Variation between days can be attributed to the variation in radiation geometry and prevailing weather conditions during the period of the experiment (Fig. 6.5).

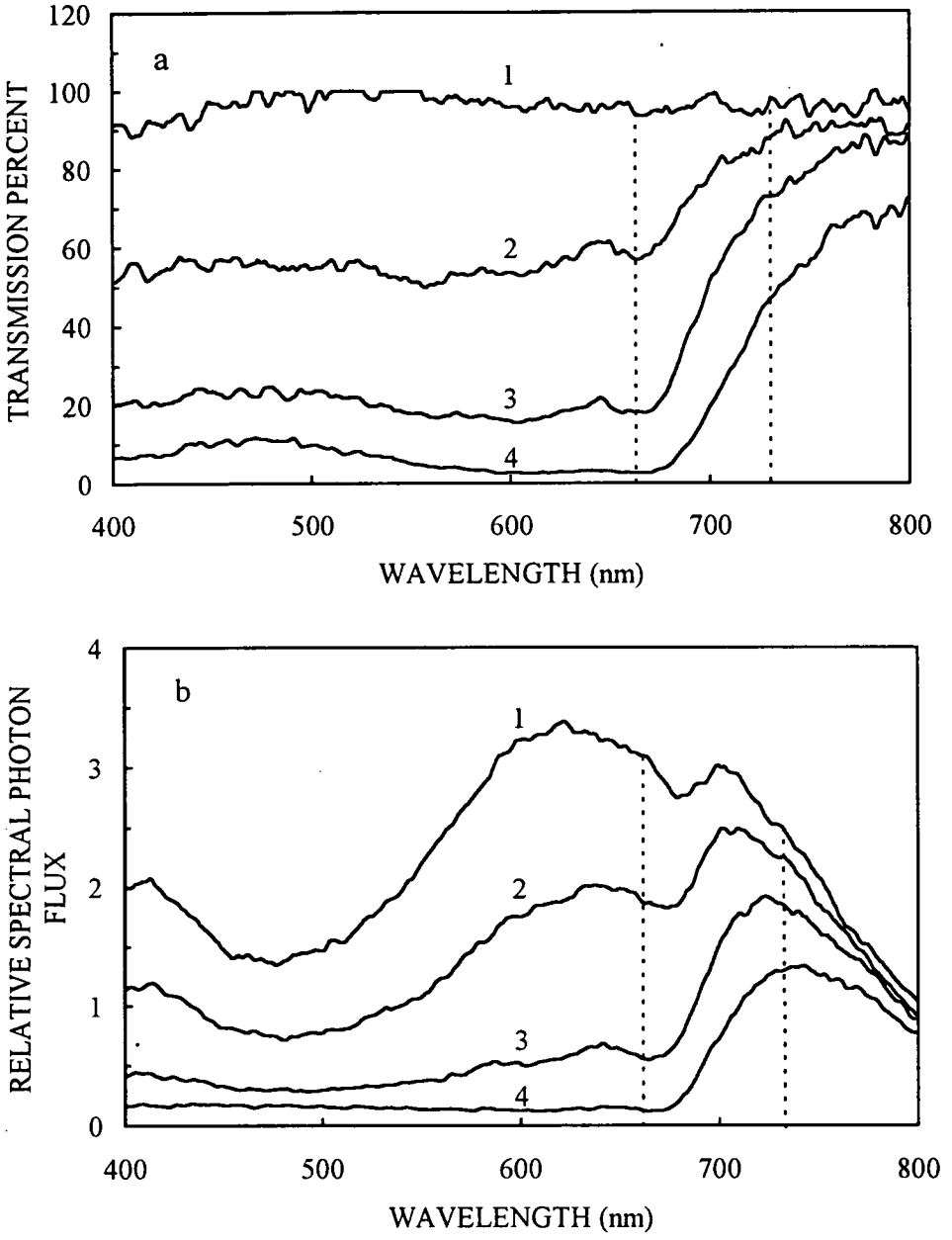

Figure 6.3 a: Transmission percent; b: relative spectral photon flux of filters used for shade-cover during the growth of *J. procera* and *A. gracilior* seedlings under different PPFs and nutrient supplies in a glasshouse. Clear filter 430 (1), one layer chromid 209 filter (2), one layer chromid 211 filter (3) and two layers chromid 211 filter (4). The area between dotted vertical bars indicate transmission % and the relative spectral density in the relevant wavelengths required to calculate the R:F-r ratios.

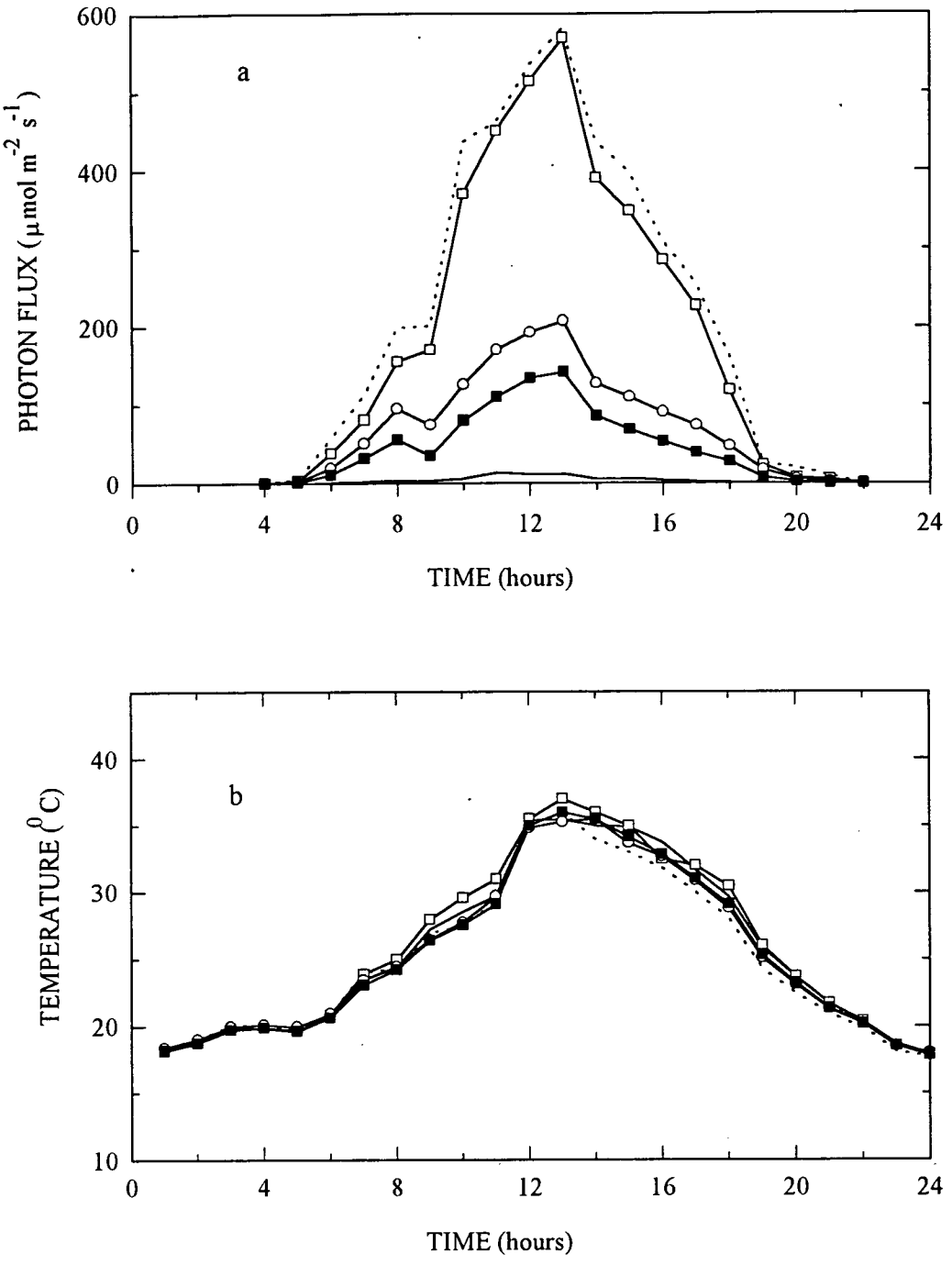

Figure 6.4: Daily pattern of a: daily photosynthetic photon flux (PPF); b: air temperatures of the open experimental bench (·····), 100% daylight (▫), 40% daylight (o), 20% daylight (▪) and 4% daylight (—) under shade-covers in a glasshouse. The data was recorded for one relatively sunny day.

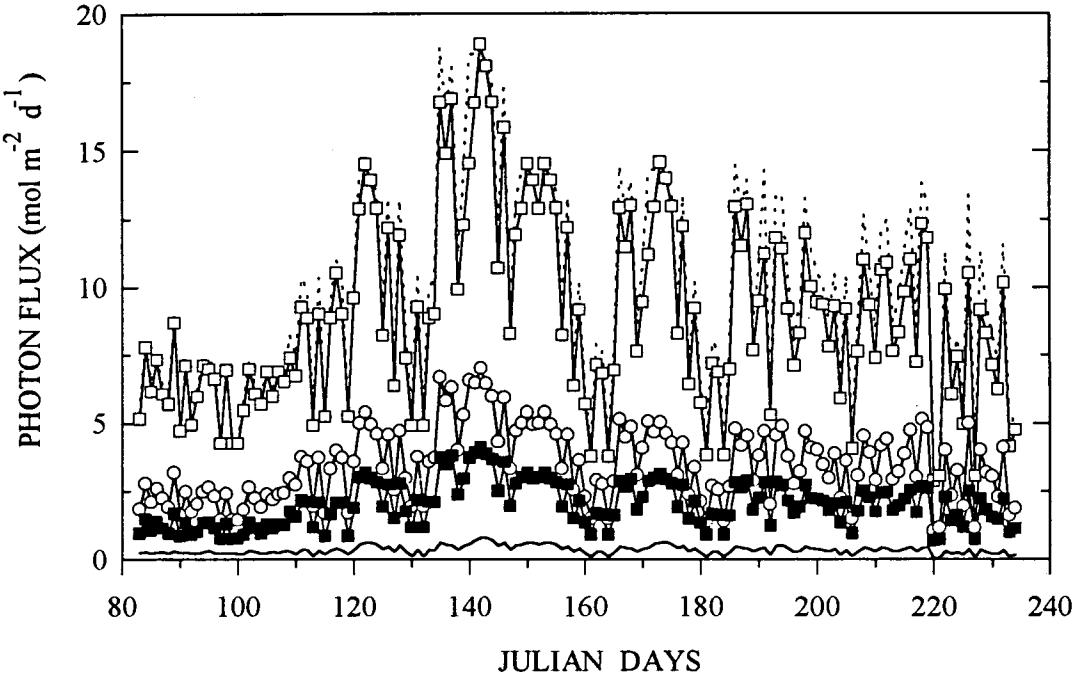

Figure 6.5: Total daily photosynthetic photon flux (PPF) of the open experimental bench (····); 100% daylight (▫); 40% daylight (o); 20% daylight (▪), and 4% daylight (—) treatments on an experimental bench in a glasshouse during the growth of *J. procera* and *A. gracilior* seedlings. The measurements were taken between March 24 and August 22, 1992.

Table 6.2: Summary of photosynthetic photon flux (mol m^{-2} d^{-1}), percent PPF transmission and R:F-r ratio of the open experimental bench and under different treatments for the duration of the experiment. Mean±SE 152 days (Fig. 6.5) observations for PPF, and mean±SE 12 readings for R:F-r ratios.

	PPF (mol m^{-2} d^{-1})			PPF (%)		R:F-r ratio	
Treatment	Mean	SE	CV%	Mean	SE	Mean	SE
Experimental bench	9.9	0.3	38	100	-	1.07	0.04
High	9.0	0.3	39	91	0.4	1.07	0.06
Medium	3.5	0.1	39	38	0.2	0.71	0.05
Low	2.0	0.1	41	22	0.2	0.29	0.01
Deep shade	0.4	0.01	44	4	0.1	0.10	0.008

Note: *Percent PPF transmission was calculated using experimental bench PPF as a reference for the high light treatment, while the clear filter was used as a reference for the other treatments. CV is percent coefficient of variation.

ii) Air temperatures

The air temperature patterns outside and inside shade-cover are shown in Fig. 6.4. The daily mean air temperature ranged from 19.6 to 42.3 ^{o}C, with the mean 28.8±0.30 for all days during the day-time and from 16.9 to 24.8 ^{o}C, with the mean 21.0±0.11 for all nights (Fig. 6.6a). Day and night air temperatures were significantly different under all treatments (Table 6.3). Temperatures were more variable during day than night, but similar between treatments. Although temperature and relative humidity were partially controlled in the glasshouse, the exact simulation of the forest air temperatures both outside and inside the shade-covers was not possible. There was no significant difference in air temperatures between treatments, though it was slightly higher in the high light treatment during day.

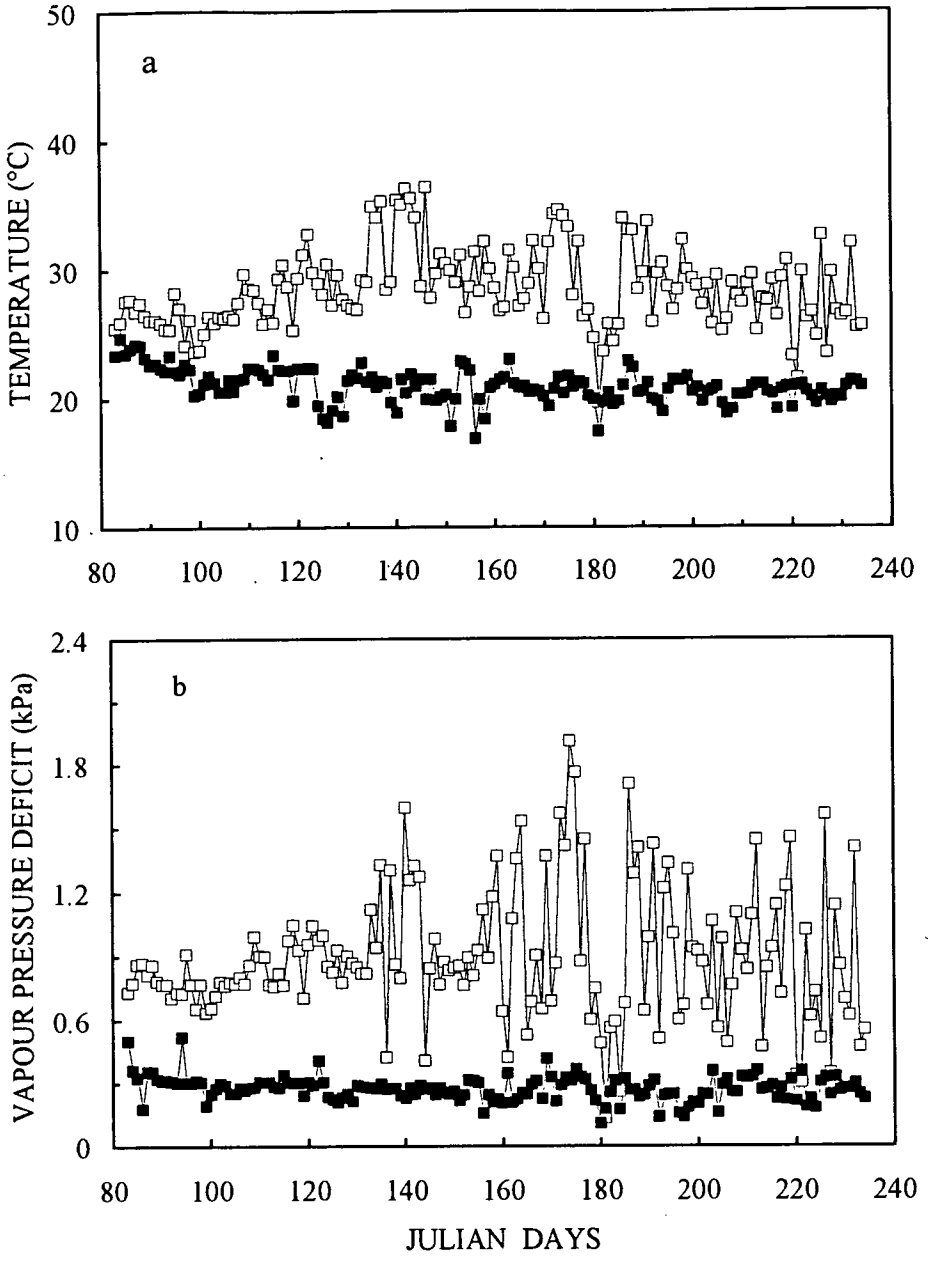

Figure 6.6: Mean day (□) and night (■) a: air temperatures b: vapour pressure deficit, in the high light treatment (clear neutral filter) on an experimental bench in a glasshouse during the growth of *J. procera* and *A. gracilior* seedlings between 24 March and 22 August, 1992.

Table 6.3: Summary of day and night air temperatures (°C) of the open experimental bench and under different light treatments for 15 days observation between April 20 and May 5, 1992.

Light Treatment	Day				Night			
	Mean	SE	Min	Max	Mean	SE	Min	Max
Experimental bench	28.9	0.1	25.0	35.7	20.6	0.2	19.0	22.3
High	31.2	1.2	26.1	39.5	20.9	0.3	19.4	23.0
Medium	30.2	1.0	26.0	37.5	20.9	0.3	19.2	22.9
Low	29.5	1.0	25.5	36.9	20.9	0.2	19.4	22.9
Deep shade	29.6	1.0	25.6	36.9	21.0	0.3	19.3	23.2

iii) Vapour pressure deficit (δe)

The daily pattern of saturation vapour pressure deficit (δe) in the high light treatment, for the duration of the experiment, is illustrated in Fig. 6.6b. The vapour pressure deficit (δe) was higher in the high light treatment and lower in the low light treatments (Table 6.4).

Table 6.4: Summary of day and night vapour pressure deficit (δe) under different light treatments for 15 days observations between April 20 and May 5, 1992.

Treatment	Day		Night	
	Mean	SE	Mean	SE
High	1.36	0.18	0.43	0.03
Medium	1.08	0.11	0.28	0.02
Low	1.07	0.14	0.29	0.02
Deep shade	0.95	0.10	0.18	0.03

6.5.2 Growth analysis

The seedlings of *J. procera* and *A. gracilior* grown under different light and nutrient levels are illustrated in Fig. 6.7. Of the seedlings originally designated for each

treatment, very few in the deep-shade treatment survived (4 seedlings in the low and 3 seedlings in the high nutrient level of each species); the majority were attacked by fungus and died after week 3 or 4. Those seedlings survived in the deep-shade remained dormant as is evident for *A. gracilior* in Fig. 6.7. Hence, the deep-shade treatment of both species was excluded from the analyses. However, the values of those seedlings surviving till harvest were included in the graphs. Therefore, the result will mainly focus on low, medium and high light treatments under both nutrient levels.

i) Biomass growth

The analysis of variance is summarised in Table 6.5. Generally, the R was significantly affected by both light and nutrient supply (Fig.6.7). The increase in *J. procera* was significant with increasing light at both nutrient levels. On the other hand, the R increase in *A. gracilior* with added nutrients was only significant at low light level. The R values were generally higher in *A. gracilior* than in *J. procera*, except at high light plus high nutrient treatment where it was slightly higher for *J. procera*. The significant positive interactions of light and nutrient in both the species indicate a synergistic effect on R by the two factors (Table 6.5).

The species showed similar patterns of response in respect to E. Light availability had an opposing effects on E and F. An increase in light resulted in an increase in E but a decrease in F, particularly in *A. gracilior* (Fig. 6.8). The relatively higher E in the high light treatment resulted in higher R in the high light treatment, despite a lower F. At low light level, the lower E was partially offset by an increase in F, particularly in *A. gracilior*. Nutrient supply had no significant effect on E in either species (Table 6.5).

The differences in F were brought about due to differences in both S and w (Fig. 6.9). The species showed quite different response in respect to S. S in *J. procera* responded to nutrients but not to light. S in *A. gracilior* responded to light but not nutrients. The effect of light was significant in *A. gracilior*. On the other hand nutrient supply had a significant effect on S in *J. procera* only (Table 6.5). The w values were the least affeted by light availability, while nutrient supply significantly increased w in both species (Table 6.5; Fig. 6.9), as evidenced by significantly increased density of foliage

Table 6.5: The effect of PPF and nutrient supply on the growth of *J. procera* and *A. gracilior* seedlings. Three-way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). Position = block; (-) = decreasing, and (+) = increasing with increasing light or nutrient supply, or positive and negative interaction effects. See also Appendix 6.1.

Variable	Level of significance: Position	Light	Nutrient	Light* Nutrient Interaction
i) *J. procera*:				
Relative biomass growth rate, *R*	ns	+***	+***	+***
Net assimilation rate, *E*	ns	+***	ns	ns
Leaf area ratio, *F*	ns	ns	+***	ns
Specific leaf area, *S*	ns	ns	+***	ns
Leaf weight ratio, *w*	ns	ns	+***	+*
Specific stem length, *L*	*	-***	-***	-**
Stem weight ratio, *s*	ns	-***	+***	ns
Root weight ratio, *r*	ns	+***	-***	+***
Number of leaves	ns	+***	+***	+***
Root:Stem length ratio	ns	+*	-***	+*
ii) *A. gracilior*:				
Relative biomass growth rate, *R*	ns	+***	+***	+**
Net assimilation rate, *E*	ns	+***	ns	ns
Leaf area ratio, *F*	ns	+***	+***	ns
Specific leaf area, *S*	ns	-***	ns	ns
Leaf weight ratio, *w*	ns	ns	+***	ns
Specific stem length, *L*	ns	-**	+**	-**
Stem weight ratio, *s*	ns	*	ns	ns
Root weight ratio, *r*	ns	ns	-***	ns
Number of leaves	ns	+***	+***	ns
Root:Stem length ratio	ns	+*	-***	+***

Figure 6.7: Photograph showing *J. procera* (upper) and *A. gracilior* (lower) seedlings grown under different light and nutrient levels for 20 weeks in a glasshouse. a & e: high light; b & f: medium light; c & g: low light, and d & h: deep-shade. Low nutrient (left) and high nutrient (right).

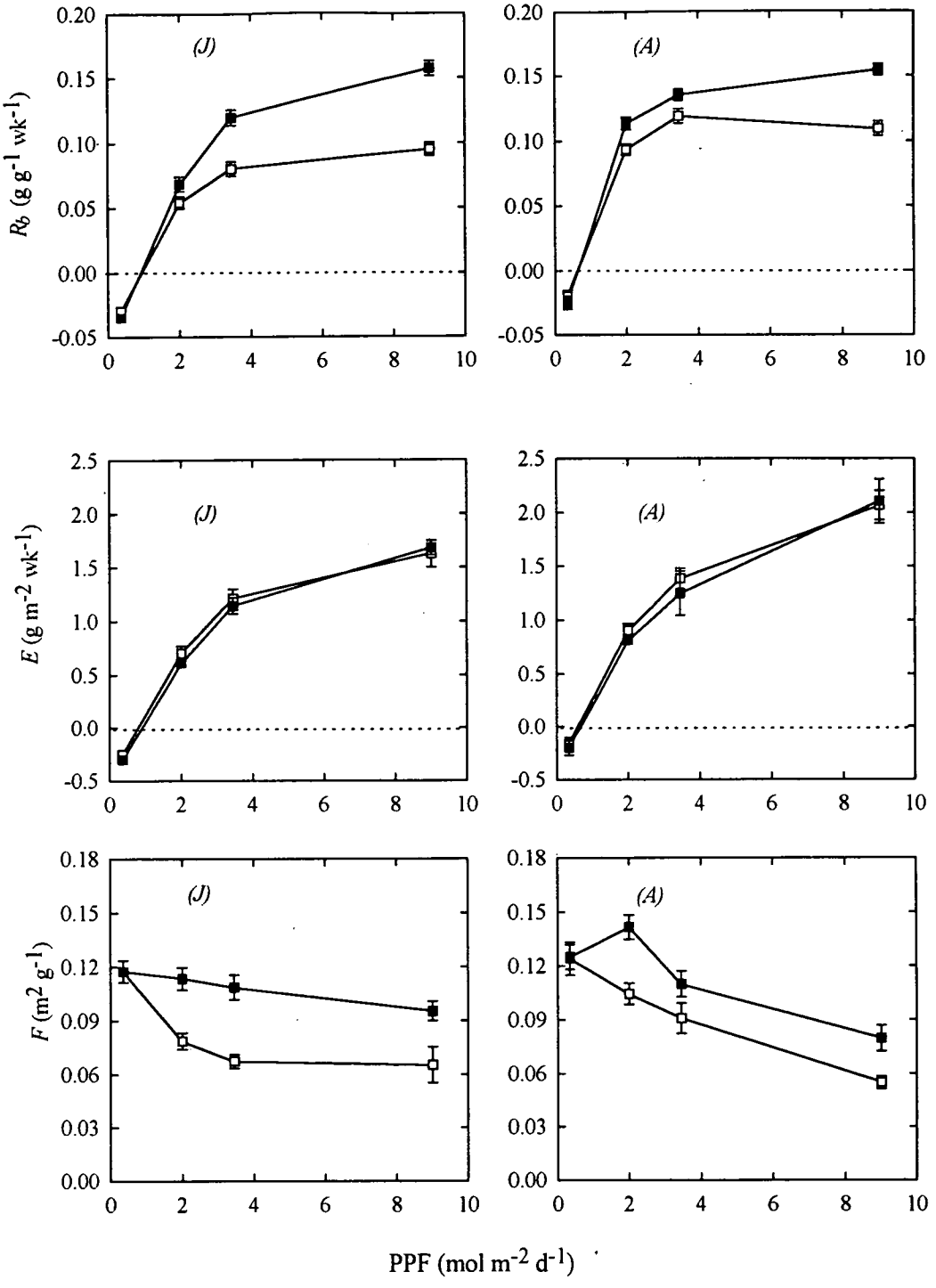

Figure 6.8: Relative biomass growth rate (upper), net assimilation rate (middle) and leaf area ratio (lower) of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient levels for 20 weeks in a glasshouse. Means of 10 seedlings; vertical bar indicates standard error of mean. See also Appendix 6.2.

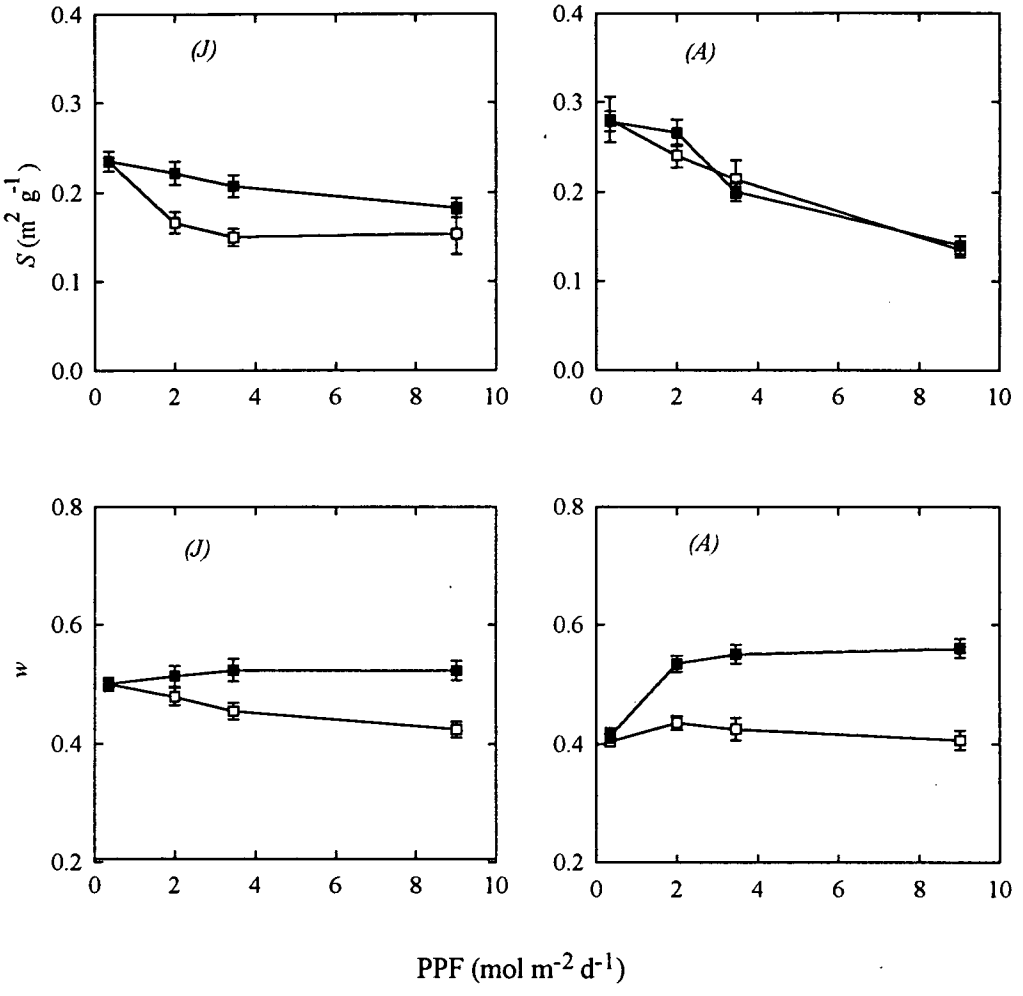

Figure 6.9: Specific leaf area (upper), and leaf weight ratio (lower) of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient levels for 20 weeks in a glasshouse. Means of 10 seedlings; vertical bar indicates standard error of mean. See also Appendix 6.2.

in both species (Fig. 6.7; Table 6.6). However, in *J. procera*, *w* was less affected by nutrient supply at low light in (Fig. 6.9). Hence, a significant interaction between light and nutrient on *w*.

Both light and nutrient supply affected allocation patterns of dry matter (Fig. 6.10). Species showed similar pattern of response to light availability but contrasting response to nutrient supply in respect of *L* (Table 6.5). *J. procera* had much greater *SSL* both in low nutrient levels and in low light levels than plants receiving both high light and nutrient. This contrasts with *L* in *A. gracilior* which showed relatively little response to nutrient, though was highest at low light levels and high nutrient levels.

The light levels had opposing effects on stem weight ratio (*s*) and root weight ratio (*r*) in *J. procera* seedlings, whereas this effect was not appreciable in *A. gracilior* seedlings (Fig. 6.10). The *s* was significantly decreased with increasing light at both nutrient levels in *J. procera* seedlings (Table 6.5). In *A. gracilior* seedlings, nutrient supply had no significant effect on *s*, while the effect of light was significant only in the seedlings growing under low light. *r* was significantly reduced by nutrient supply in both species, while a significant effect of light was demonstrated only in *J. procera* (Fig. 6.10; Table 6.5). The *r* values in *J. procera* seedlings, increased with increasing light at both nutrient levels. The root system of *A. gracilior* displayed important differences in respect to root:stem length ratio (Table 6.6; Fig. 6.7). It produced a higher root:stem length ratio in low nutrient. At the high nutrient level, there was no response to increasing light. At low nutrient levels, however, both species showed significantly increasing root:stem length ratio with increasing light (Table 6.6). Also *J. procera* seedlings had a much longer tap-root and larger number of secondary and tertiary roots at high light level than *A. gracilior* seedlings, which had much shorter tap-root and were the least branched (Fig. 6.7).

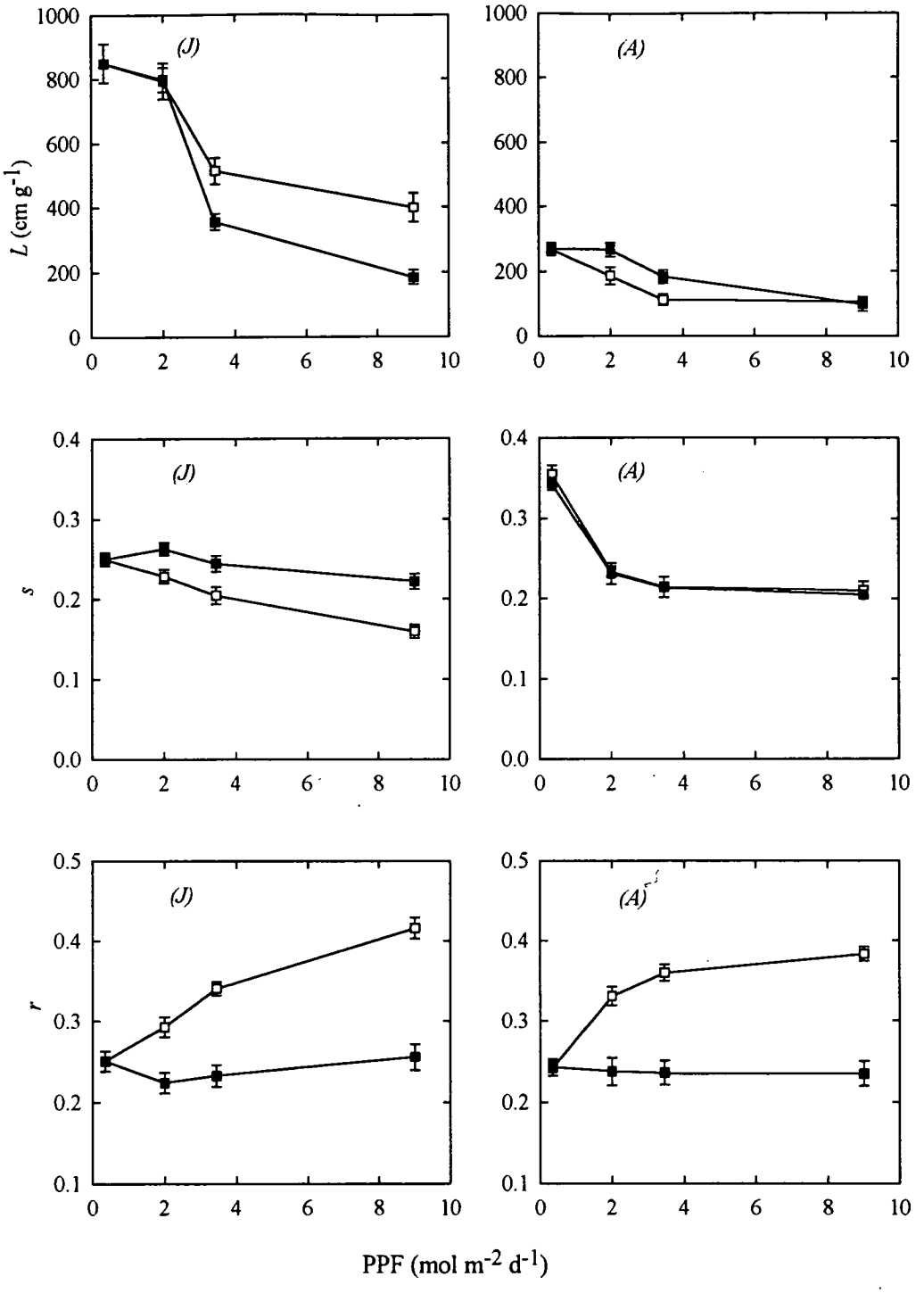

Figure 6.10: Specific stem length (upper), stem weight ratio (middle) and root weight ratio (lower) of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient levels for 20 weeks in a glasshouse. Means of 10 seedlings; vertical bar indicates standard error of mean. See also Appendix 6.2.

Table 6.6: The effect of PPF and nutrient supply on number of leaves and root:stem length ratio of *J. procera* and *A. gracilior* seedlings. Mean±SE of 10 seedlings. Duncan's multiple range test on each species separately. Means preceded by the same letter are not significantly different from each other at $P \leq 0.05$.

PPF (mol m-2 d-1)	*J. procera* Nutrient level Low	*J. procera* Nutrient level High	*A. gracilior* Nutrient level Low	*A. gracilior* Nutrient level High
i) Number of leaves:				
2.0	d95±3	c108±2	d35±2	cd45±3
3.5	c108±5	b128±4	cd44±2	b61±3
9.0	c102±3	a139±5	bc50±4	a82±9
ii) Root:stem length ratio:				
2.0	c3.7±0.2	c3.2±0.2	b2.7±0.2	c1.5±0.1
3.5	b4.5±0.1	c3.0±0.2	a3.5±0.4	c1.6±0.2
9.0	a5.2±0.1	c3.4±0.1	a3.7±0.3	c1.4±0.1

ii) Height growth

In general, although few seedlings survived in the deep-shade treatment, light availability had no significant effect on height growth of *J. procera* seedlings, while there was a significant interaction effect in *A. gracilior* seedlings between light and nutrients (Fig. 6.7; Table 6.7; Fig. 6.11). Both species responded positively and significantly to nutrient supply. There was a significant and progressive increase in *A. gracilior* seedlings with increasing light at high nutrient level, and a decrease at low nutrient level (Fig. 6.7).

Fig. 6.12 illustrates the trend of stem extension of both species against time in response to different light and nutrient supply. The importance of the information provided is not whether it is significant or not but the behaviour of the species under different treatments at different stages of development. This is valuable in planning the nature and timing of activities both at the nursery and field for artificial and natural regeneration. Seedlings that survived under deep-shade treatment completed their

Table 6.7: The effect of PPF and nutrient supply on the relative stem extension rate (*RGR*) of *J. procera* and *A. gracilior* seedlings. Three-way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq .01$; * $P \leq 0.05$). Position = block; (-) = decreasing, and (+) = increasing with increasing light or nutrient supply, or positive and negative interaction effects. See also Appendix 6.1.

		Level of significance		
Variable	Position	Light	Nutrient	Light*Nutrient Interaction
Juniperus procera	ns	ns	+***	ns
Afrocarpus gracilior	ns	+***	+***	+***

hypocotyl growth and remained dormant after the second week. *J. procera* seedlings grown under low nutrient had similar growth under all light treatment until week 8 when seedlings in low and medium light started to gain height faster than those seedlings under high light. This suggest that seedlings under all conditions were using their stored food for the first three weeks, and an increased height growth was brought about by reduced light under low nutrient conditions (Fig. 6.12a). Under high nutrient conditions, however, *J. procera* seedlings in the high light treatment showed reduced height growth until week 12 and overtook the seedlings under low light by week 13 and the seedlings in the medium light by week 18 (Fig 6.10b).

The pattern of extension growth is slightly different and simpler in *A. gracilior* (Fig. 6.12 c, d). At low nutrient supply, seedlings grown under reduced light maintained higher stem extension rates than those grown under high light throughout the experiment (Fig. 6.12 c). In contrast, seedlings in the high nutrients treatment showed a positive response to increasing light from week 7 onwards.

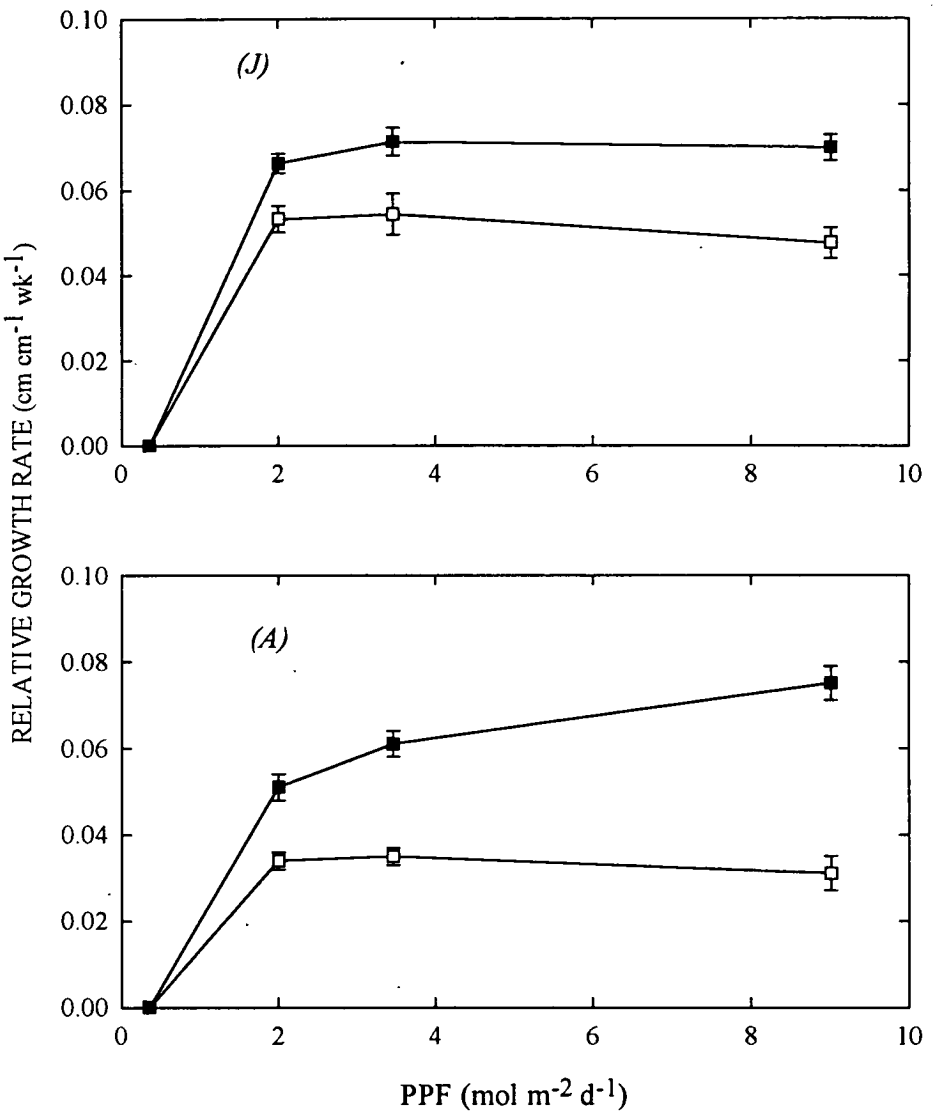

Figure 6.11: Relative stem extension rate of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient levels for 20 weeks in a glasshouse. Mean of 10 seedlings; vertical bar indicates standard error of mean. See also Appendix 6.2.

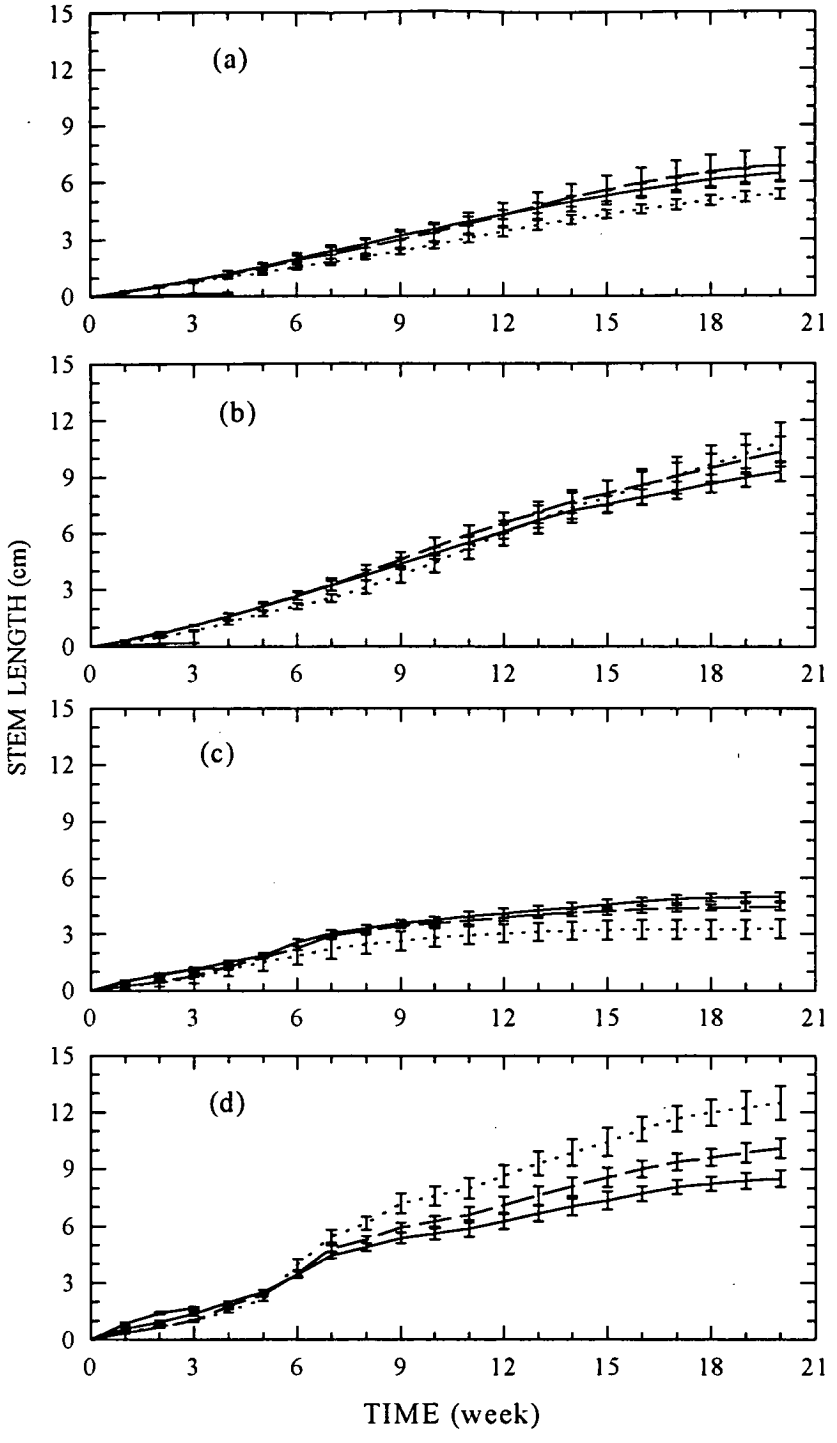

Figure 6.12: Stem extension of *J. procera* (a and b); and *A. gracilior* (c and d) seedlings grown under varying PPF and nutrient levels in a glasshouse for 20 weeks. High (·····); medium (– – –); low (——), and deep-shade (-·-·-) light. Low nutrient (a and c) and high nutrient (b and d). Mean of 10 seedlings; vertical bar indicates standard error of mean.

6.5.3 Leaf anatomy

The differences in relative biomass growth rates were accompanied by differences in leaf anatomy (Table 6.8). In general, there was a significant increase in leaf thickness with increasing light in both species (Fig. 6.13). This was due to the significant increase both in palisade tissue and spongy mesophyll. The relative increases in thickness was greater in *J. procera* than in *A. gracilior*. There was a general tendency of the palisade:spongy ratio to increase with increasing light, but the difference was only significant at high light in *J. procera*, and low to medium light in *A. gracilior* seedlings (Fig. 6.14). In general, nutrient supply had no significant influence on leaf thickness (Table 6.8).

The leaves of both species are amphistomatous but with many more stomata on the lower than upper leaf surface in *A. gracilior* seedlings, particularly at low nutrient plus high light level (Fig. 6.14). Overall, stomatal density was affected by light availability in both species though there was no overall effect of nutrients (Table 6.8). The increase was highly significant in *A. gracilior* and just significant in *J. procera* (Fig. 6.14).

6.5.4 Leaf dry weight and leaf chlorophylls contents

The results of the analysis of variance of leaf dry weight, leaf chlorophyll and nitrogen contents are summarised in Table 6.9. Leaf dry weight increased significantly with increasing light in both species (Fig. 6.15). In contrast, nutrient supply decreased leaf dry weight per unit area. There was a significant interaction between the two factors in *J. procera*.

Light had no significant effect on chlorophyll contents in *J. procera* seedlings, when expressed on a leaf area basis (Table 6.9). In *A. gracilior* seedlings, however, total chlorophyll (chlorophylls $a + b$) and chlorophyll a were significantly lower in reduced light, particularly at low nutrient level, while there was no significant difference in chlorophyll b (Table 6.9; Fig. 6.15; 6.14). On the other hand, nutrient supply had a significant effect on chlorophyll content in on both species, except for chlorophyll b in *J. procera*, which was not affected significantly (Table 6.9).

Table 6.8: The effect of PPF and nutrient supply on the leaf characteristics of *J. procera* and *A. gracilior* seedlings. Three-way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq .01$; * $P \leq 0.05$). Position = block; (-) = decreasing, and (+) = increasing with increasing light or nutrient supply, or positive and negative interaction effects. See also Appendix 6.3.

Variable	Level of significance			
	Position	Light	Nutrient	Light* Nutrient Interaction
i) *J. procera:*				
Leaf thickness (μm)	ns	+***	ns	ns
Palisade thickness (μm)	ns	+***	ns	ns
Spongy mesophyll (μm)	ns	+***	ns	ns
Palisade:Spongy ratio	ns	+***	ns	ns
Stomatal density (mm^{-2})	ns	+*	ns	ns
ii) *A. gracilior:*				
Leaf thickness (μm)	ns	+***	ns	ns
Palisade thickness (μm)	ns	+***	ns	ns
Spongy mesophyll (μm)	ns	+***	ns	ns
Palisade:Spongy ratio	ns	+*	ns	ns
Stomatal density (mm^{-2})	ns	+***	ns	-*

This comparison became somewhat different when chlorophyll levels are expressed on a leaf weight basis (Table 6.9). Total chlorophyll, and chlorophyll *a* and *b* of both species were significantly affected by both light availability and nutrient supply except for chlorophyll *b* in *J. procera*. It is evident from Fig. 6.16 and 6.15 that plants grown in low light developed more chlorophyll per gram of leaf, and that this effect is more pronounced in *A. gracilior*.

The chlorophyll *a:b* ratio was not significantly affected by light availability in either species, while nutrient supply significantly increased the ratio in *J. procera* seedlings (Table 6.9).

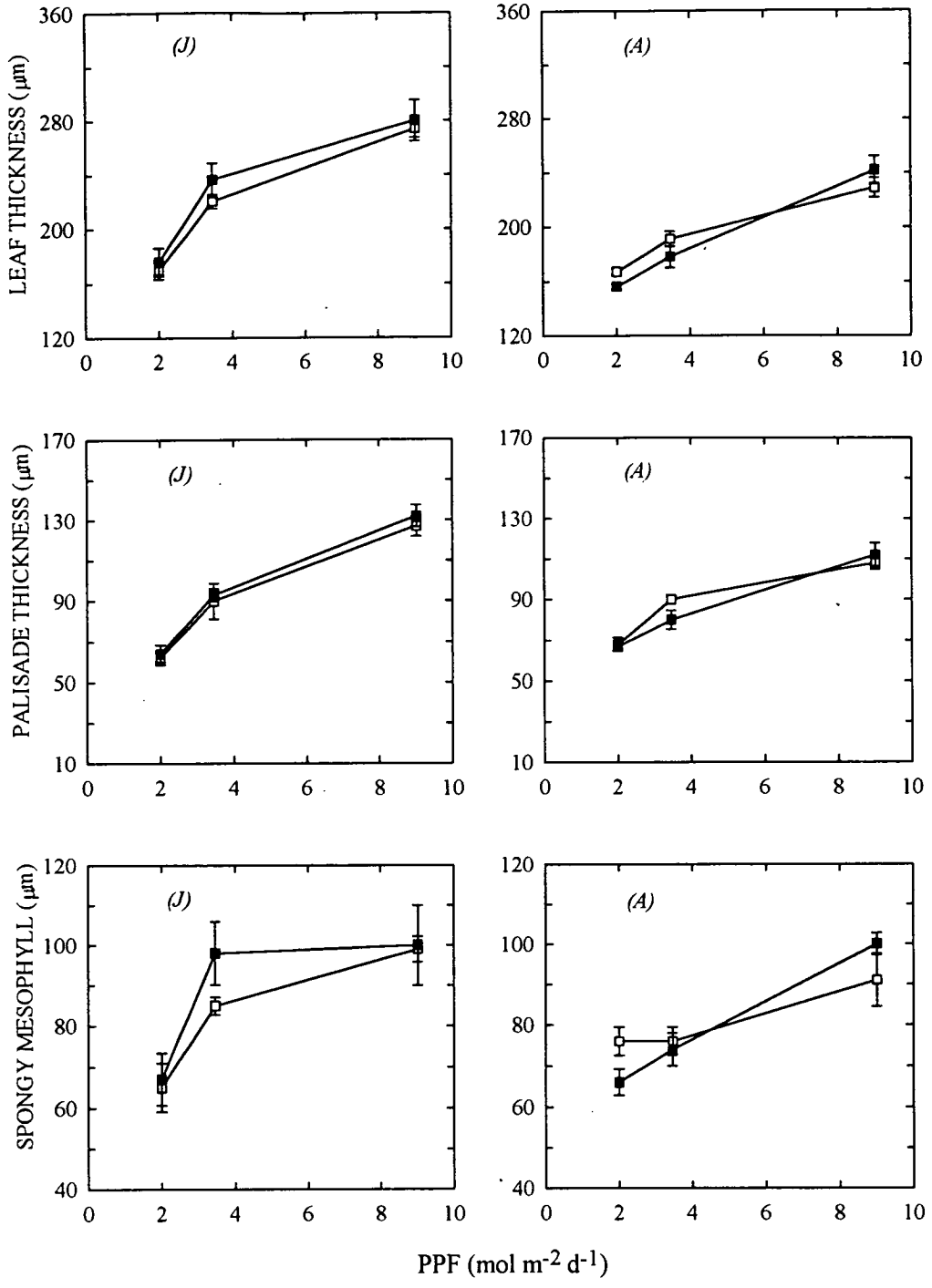

Figure 6.13: Effect of PPF and nutrient supply on leaf thickness; palisade thickness, and spongy mesophyll of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient treatment for 20 weeks in a glasshouse. Mean of 10 seedlings; vertical bar indicates standard error of the mean. See also Appendix 6.4.

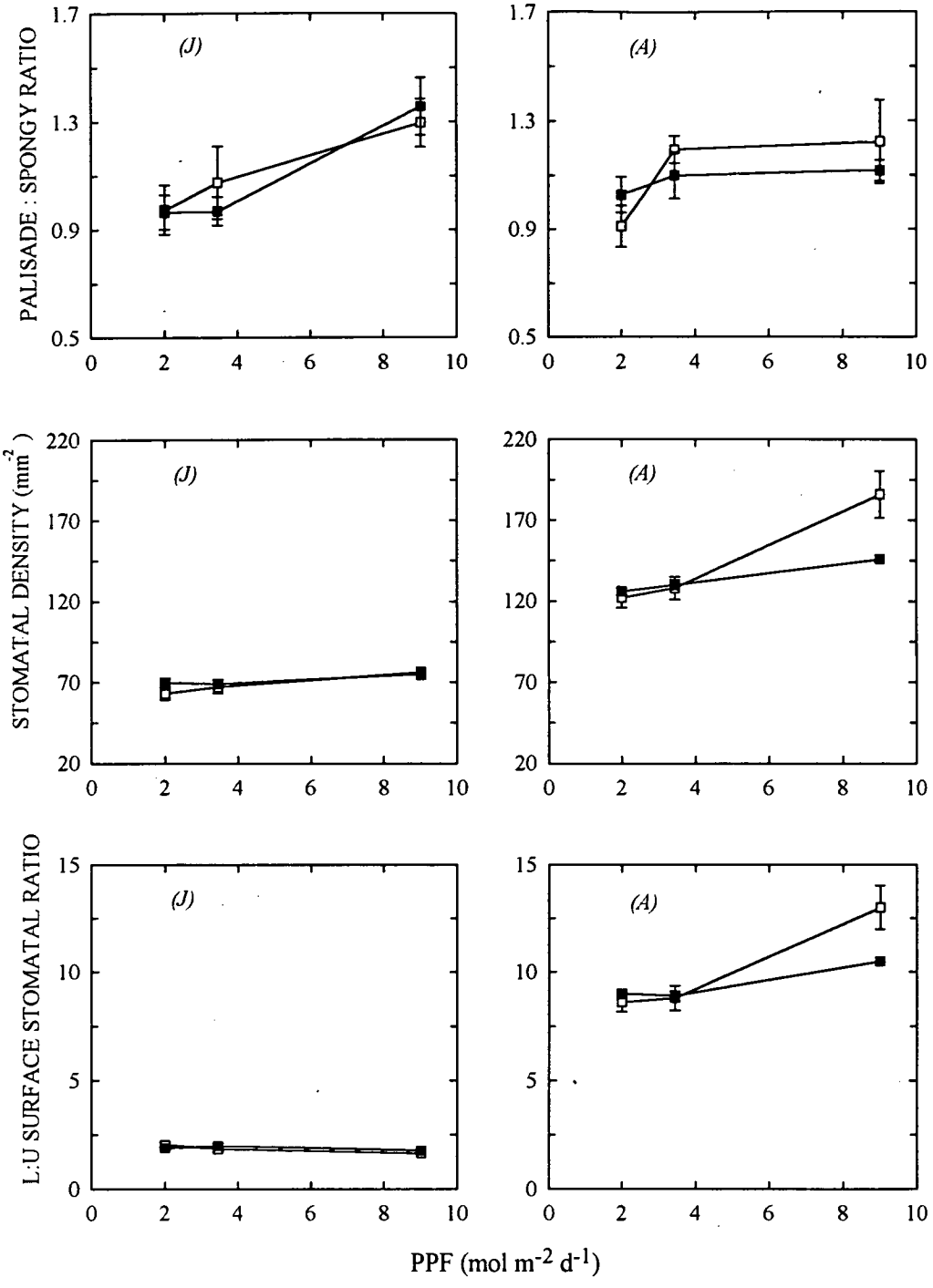

Figure 6.14: Effect of PPF and nutrient supply on palisade:spongy ratio; stomatal density, and lower:upper leaf surface stomatal density ratio of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient treatment for 20 weeks in a glasshouse. Mean of 10 seedlings; vertical bar indicates standard error of the mean. See also Appendix 6.4.

Table 6.9: The effect of different PPF and nutrient supply on the leaf dry weight, leaf chlorophylls and leaf nitrogen content of *J. procera* and *A. gracilior* seedlings for 20 weeks in a glasshouse. Three-way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq .01$; * $P \leq 0.05$). Position = block; (-) = decreasing, and (+) = increasing with increasing light or nutrient supply, or positive and negative interaction effects. See also Appendix 6.5.

Variable	Level of significance			
	Position	Light	Nutrient	Light* Nutrient Interaction
i) *J. procera:*				
Leaf dry weight per unit leaf area, (g m^{-2})	ns	+***	+***	-*
Leaf chlorophylls (mg m^{-2}):				
a+b	ns	ns	+***	ns
a	ns	ns	+***	ns
b	ns	ns	ns	ns
Leaf chlorophylls (mg g^{-1}):				
a+b	ns	-***	+***	ns
a	ns	-***	+***	ns
b	ns	-***	+*	ns
a:b ratio	ns	ns	+***	ns
Leaf nitrogen % per mass	ns	-***	+***	ns
ii) *A. gracilior:*				
Leaf dry weight per unit leaf area, (g m^{-2})	ns	+***	ns	ns
Leaf chlorophylls (mg m^{-2}):				
a+b	ns	-*	+***	ns
a	ns	-*	+***	ns
b	ns	ns	+***	ns
Leaf chlorophylls (mg g^{-1}):				
a+b	ns	-***	+***	ns
a	ns	-***	+***	ns
b	ns	-***	+***	ns
a:b ratio	ns	ns	ns	ns
Leaf nitrogen % per mass	ns	ns	+***	ns

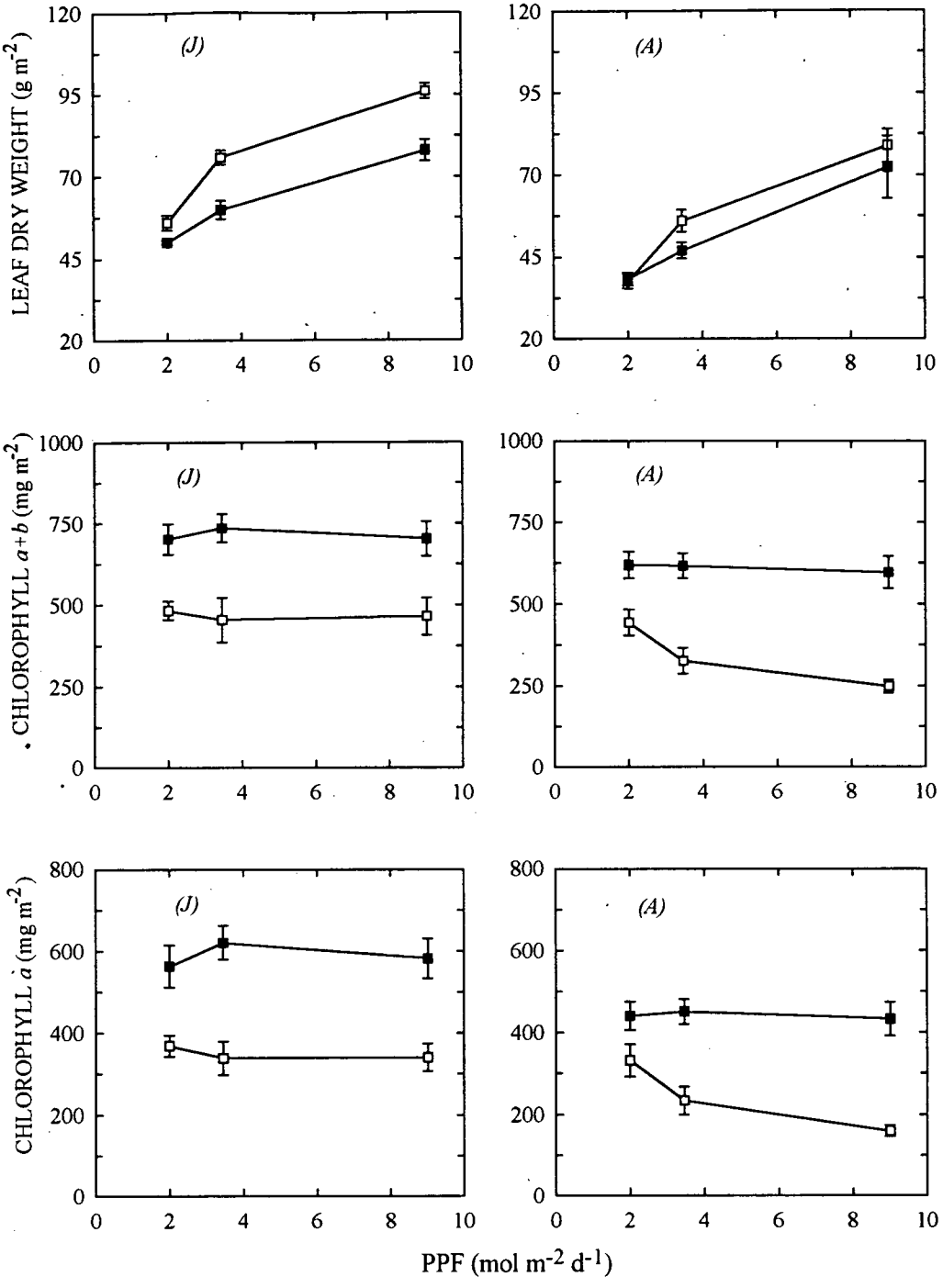

Figure 6.15: Effect of PPF and nutrient supply on leaf dry weight, total chlorophylls *a*+*b* (mg m^{-2}), and chlorophyll *a* (mg m^{-2}) contents of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient treatments for 20 weeks in a glasshouse. Mean of 10 seedlings; vertical bar indicates standard error of the mean. See also Appendix 6.6.

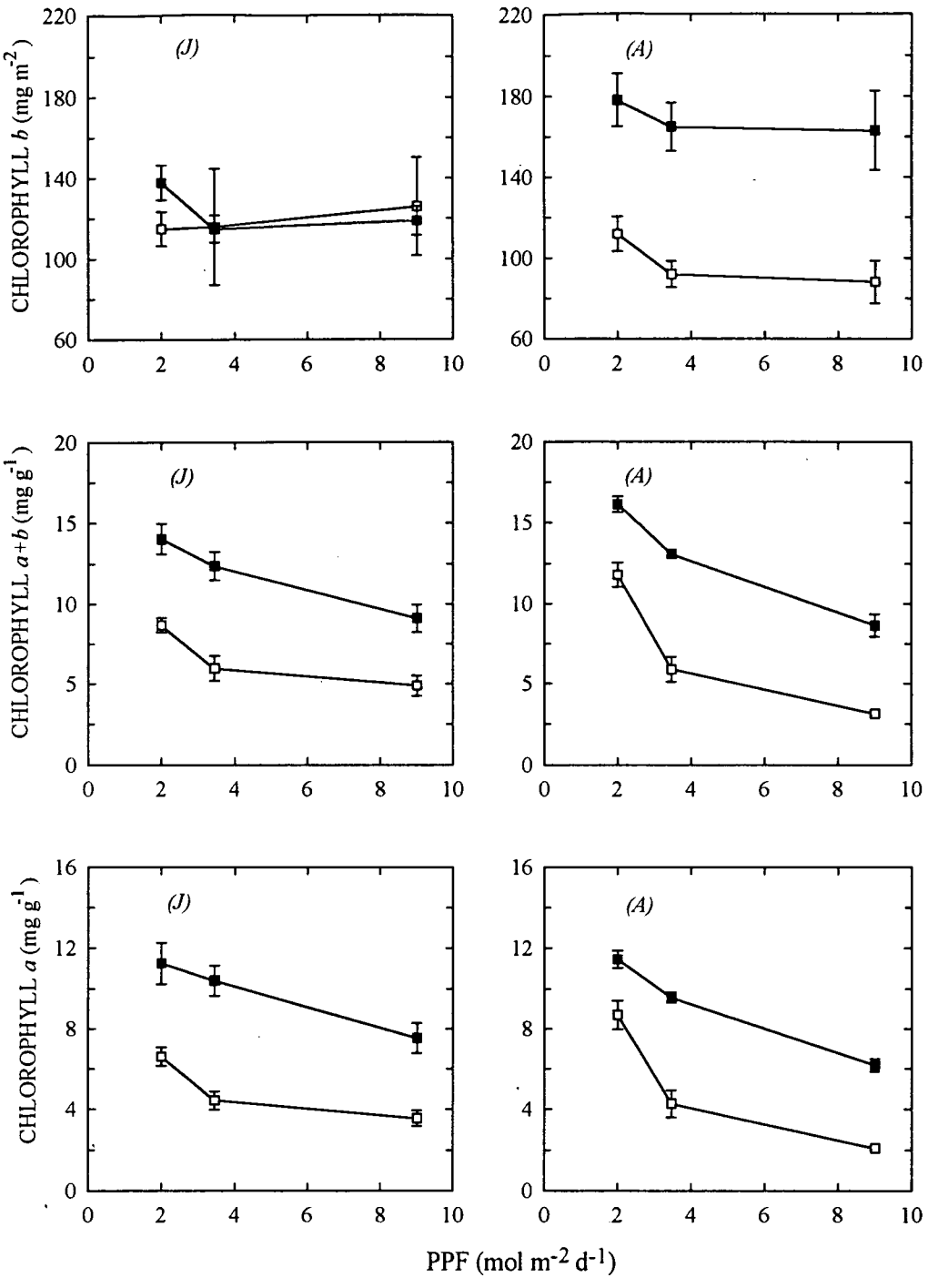

Figure 6.16 Effect of PPF and nutrient supply on leaf chlorophyll *b* (mg m^{-2}); leaf chlorophylls *a*+*b* (mg g^{-1}), and chlorophyll *a* (mg g^{-1}) of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient treatments for 20 weeks in a glasshouse. Mean of 10 seedlings; vertical bar indicates standard error of the mean. See also Appendix 6.6.

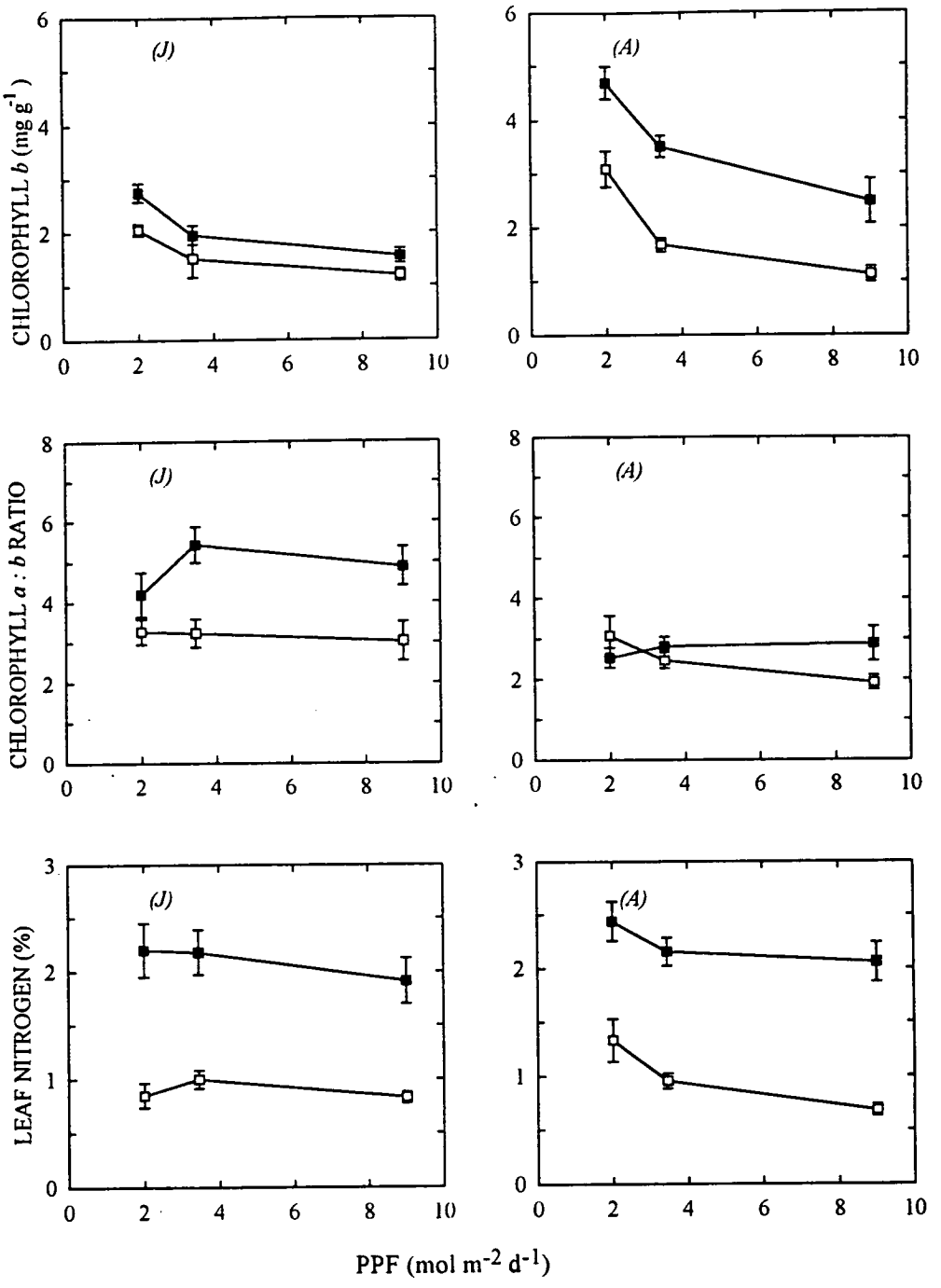

Figure 6.17 Effect of PPF and nutrient supply on leaf chlorophyll *b* (mg g-1); leaf chlorophylls *a:b* ratio, and leaf nitrogen (% oven-dry weight) content of *J. procera (J)* and *A. gracilior (A)* seedlings grown under high (▪) and low (▫) nutrient treatments for 20 weeks in a glasshouse. Mean of 10 seedlings; vertical bar indicates standard error of the mean. See also Appendix 6.6.

6.5.5 Leaf nitrogen content

Leaf nitrogen content was not significantly affected by light availability in *J. procera*. In contrast, nitrogen contents of *A. gracilior* seedlings were significantly reduced with increasing light level (Table 6.9; Fig. 6.17). Nitrogen contents in both species were significantly increased by nutrient supply.

6.6 Discussion

6.6.1 Evaluation of experimental conditions

In general, levels of PPF as low as those found at the forest floor of Arba-gugu were achieved for the low and medium light treatments in the glasshouse. The deep-shade treatment of about 1% of the open light condition of Arba-gugu, was lower than those recorded in the forest floor (Section 3.4.1). Though the experiment was conducted during spring and summer months, when light levels are expected to be high, the open light level treatment was not very high and on the average only about 31% of the Arba-gugu open (large clearing) light flux and about 78% of that at the gap edge were recorded (Section 3.4.1). So the high light level treatment, used in this experiment, equates to the edge of the clearing of Arba-gugu. The R:F-r ratios found at the open and in the forest floor of Arba-gugu were achieved for all treatments except for the deep-shade treatment, which was extremely low as was the PPF. The photoperiod, of about 12 hours at the start of the experiment increasing to about 14 hours for the later part of the experiment, was actually longer than the Arba-gugu conditions.

Typically, day-time air temperatures were highest in the large clearing and lowest in the forest understorey habitats of Arba-gugu forest (Section 3.4.2). Although air temperatures were controlled in the glasshouse, the exact simulation in respect of temperatures in the high, medium, low light and deep-shade treatments was not obtained. However, there was no significant difference in temperatures between treatments either during day or night (Table 6.2). Temperatures in the glasshouse were generally higher, particularly after April as the experiment was extended to the

summer months, and are close to the high temperature days recorded in Arba-gugu forest (Section 3.4.2).

6.6.2 Effect of shade and nutrients

The effects of light and nutrient supply on seedlings are reflected in differences in R and seedling survival. In deep shade, both *J. procera* and *A. gracilior* seedlings were below their light compensation point, E and R being negative (Fig. 6.8). Most seedlings of both species, lost some of their lower leaves and over 60% of the seedlings were attacked by fungus and died in week 3 and 4. The remaining 30 to 40% of seedlings under this treatment neither increased in growth nor produced new leaves or roots, nor any extension of the stem, other than completing their hypocotyl growth. This means that seedlings of both species do not tolerate shade light as low as 1% of the open PPF condition of Arba-gugu.

At lower PPF, both species maintained a positive R and E and displayed similar modes of adaptation (Table 6.6). In *A. gracilior*, however, there was a significant increase in F with reduced light intensity resulting from a significantly higher S (Fig. 6.8; 6.7). As against high light it resulted in about a 1.8 times increase in F, compared to 1.2 times increase in *J. procera*. E was significantly higher in seedlings of *A. gracilior* than those of *J. procera* at low light levels. The seedlings showed almost no change in w over the range of PPFs used (Fig. 6.9). The much less leafy nature of *J. procera* in comparison with *A. gracilior*, however, was due almost entirely to the relatively greater density of the *J. procera* leaves and hardly at all to any variation in w which, in fact, showed a small difference in favour of *J. procera* under low nutrient (Fig. 6.8; 6.7). An increase in S combined with an almost equal w in *A. gracilior*, led to an increased F. This relative increase in leaf area compensated, at least partially, for a lower photosynthesis per unit area under low light levels. In this way, F made a significant contribution in maintaining a positive R at low light levels. As shown in Fig. 6.8, a positive R in the low light level was highly influenced by E. The seedlings of both species show such an adaptation to low light (Corré 1983b; Pompa and Bongers, 1988). F had no effect on R, when the value of E was very low, and this generally happens with pioneer seedlings growing in deep forest shade (Pompa and Bongers, 1988). Hence, the higher increase in F with decreasing light level in

A. gracilior, is evidence of a more positive adaptation to low light at the whole seedling level compared to *J. procera*. Compared to the Arba-gugu forest understorey light conditions, the low light treatment used in this experiment (Table 6.2) was about 7% of the large clearing, which is comparable to the low understorey light conditions of Arba-gugu forest (Section, 3.4.1).

At the high PPF levels, the low nutrient supply caused a larger decrease in R (Fig. 6.8), significant for *A. gracilior* seedlings. A lower F appeared to be largely responsible for this decrease in the seedlings of *A. gracilior*, because E remained almost unaffected by nutrient supply. But in the *J. procera* seedlings, the decrease of R was the consequence of a lower w. The photosynthetic apparatus of the plants receiving a low nutrient supply is markedly less efficient than those receiving a high nutrient supply under the high light conditions (Robson and Parsons, 1978). The nutrient supply, on the other hand, lifts leaf N status regardless of light level during growth, and photosynthesis responds accordingly (Thompson *et al.*, 1988). *J. procera* seedlings grown under low light level had relatively lower leaf N content than those grown under high nutrient levels. *A. gracilior* seedlings, on the other hand, had a decreasing leaf nutrient contents with increasing light level. The leaves under low light level require less RuBP carboxylase, hence less leaf N, to sustain light saturated photosynthesis in that light condition compared with the leaves of those seedlings growing in the high light levels (Björkman, 1981). With this advantage, the seedlings receiving low nutrient supply displayed almost the same E as their higher-nutrient counterparts under the low light.

Seedlings grown under high light and low nutrient supply were morphologically very different as a result of biomass allocation pattern. Also seedlings receiving low nutrient supply at high light level produced yellowish-green foliage. The substantial increase in L in *J. procera* seedlings grown under higher light levels plus low nutrient supply may indicate the lower capacity for increasing photosynthetic enzyme. Also, they had a higher s at lower light level than those at higher light level. This means that seedlings receiving a low nutrient supply produced the same length of stem with less material at the higher light levels compared to those seedlings grown under high nutrient. In contrast, *A. gracilior* seedlings grown under high nutrient level displayed a higher L than those under the low nutrient plus lower light level. It may be

speculated that the stem cell enlargement was enhanced with the supply of high nutrient resulting in a relatively low density stem tissue, and hence a higher L value.

The higher L in *J. procera* compared with *A. gracilior* may also be influenced by the way biomass is partitioned between plant parts indicating the level of shade-tolerance. In exposure-intolerant species, photosynthate is allocated preferentially to leaf growth, and then to roots, storage and stem growth as carbon availability increases. Thus the faster-growing seedlings in gaps will allocate more biomass to stem growth, thereby increasing height growth and competitive ability when more carbon is available, while slow-growing seedlings in shade will allocate most of their above-ground growth to leaves (Waring and Pitman, 1985).

Seedlings grown under a low rate of nutrient supply demonstrated an increased proportion of root, expressed as the root weight ratio (r). The r in *J. procera* was at the expense of both leaf and stem, whilst the increase in *A. gracilior* was at the expanse of leaf (Fig. 6.9; 6.8). This is evident as *A. gracilior* seedlings produced similar s under both nutrient supply (Fig. 6.10). Also, at higher PPF the r in *J. procera* increased more certainly than in *A. gracilior*. Changes in environmental conditions are met by allocation of growth resources to the organ that is capable of alleviating the limitation imposed by the new condition (Corré, 1983; Thompson *et al.*, 1988). This means that *J. procera* is more responsive to changes in environment and channels more of its resources to roots (Fig. 6.10).

6.6.3 Leaf characteristics and chlorophyll levels

Seedlings and saplings, underneath a canopy of forest vegetation experience low photon flux all the time unless canopy openings allow sunflecks. It is also known that the leaves of such shaded plants are thinner and have larger chloroplasts which are richer in chlorophyll than leaves of plants in the open (Börkman and Holmgren, 1963; Börkman, 1968). Higher specific leaf area is a major characteristic of leaves of plants developed under low as against high photon fluxt. Once leaves have formed, adaptation can only be achieved substantially by chlorophyll or structural changes leading to alterations in leaf thickness. Furthermore, as specific leaf area is dependent on the level of light available, the chlorophyll content per unit weight is also

dependent on the level of light available during growth. Under all conditions the chlorophyll ($a + b$) content on a weight basis was higher at low light than at high light. In this experiment, there was a tendency for chlorophyll a:b ratio to be higher with decreasing light under low nutrient and vice versa under high nutrient seedlings. Boardman (1977) suggested that if chlorophyll content was expressed as per unit leaf area, it frequently would be lower in shade species and shade leaves. Lewandowska and Jarvis (1977), however, reported that on a leaf area basis there was no significant difference between chlorophyll content for sun and shade leaves of Sitka spruce because of the compensating variations in specific leaf area.

The differences in mesophyll thickness may also help to explain the differences between seedlings grown under low and high light level. Since the thicker leaves of the high light seedlings contain more chlorophyll and more chloroplast per unit area, light saturation of photosynthesis would be expected to occur only at higher light levels. This is because chloroplast shading can occur within the mesophyll layers just as mutual shading occurs among leaves within a canopy. The low light seedlings of both species had greater chlorophyll content than seedlings grown under high light level. Since at low light the light harvesting capacity of photosynthetic apparatus limits photosynthetic rate, seedlings grown in low light might have had higher photosynthetic rates than the high light seedlings. However, the increase in mesophyll per unit area in the high light seedlings may more than compensate for their lower content of chlorophyll so that the photosynthetic rate per unit area may be higher in the high light seedlings. The increase in chlorophyll a to b is associated with changes in the light-harvesting chlorophyll a to b protein.

The total chlorophyll content of the Afromontane coniferous tree species, in the present study, was within the range of other species reported by other workers. Šesták (1971) reports that normal leaves contain 100-1000 mg m^{-2} of chlorophyll ($a + b$) content. Other workers also reported values within this range (e.g. Masarovicová and Eliáš, 1980; Morales *et al.*, 1982; Kwesiga, 1984; Kamaluddin, 1991). In a review by Björkman (1981) the average chlorophyll content for 49 sun and shade plants grown under a wide range of light levels, was 485 mg m^{-2}. In this experiment, *J. procera* seedlings had a higher chlorophyll content than *A. gracilior* seedlings. The differences in these two tree species in chlorophyll content were not

only dependant on whether they were grown under low or high light but also on nutrient supply. Generally, *J. procera* had a higher chlorophyll content on a leaf area basis. The chlorophyll content varied from 248 mg m^{-2} under high light plus low nutrient to 619 mg m^{-2} under low light plus high nutrient in *A. gracilior*; while it was from 455 to 701 mg m^{-2} under similar conditions for *J. procera*. On a dry weight basis, *A. gracilior* had a higher chlorophyll content than *J. procera* at low and medium light levels, while they had similar chlorophyll content at high light level.

In this experiment, chlorophyll *a:b* ratio was much higher in *J. procera* seedlings than *A. gracilior* seedlings, and varied between 1.91 to 3.07 in *A. gracilior*, and between 3.02 to 5.43 in *J. procera* (Fig. 5.15). The ratio was generally higher under low light plus low nutrient, particularly in *A. gracilior* seedlings. In contrast, it was lower in seedlings under low light plus high nutrient. According to Šesták (1971) the chlorophyll *a:b* ratio for normal leaves is generally between 1.5 to 3.0. Masarovicová and Eliáš (1981) reported a ratio of above 3.0 for sun leaves and below 3.0 in shade leaves, and suggested that this ratio might be a good leaf characteristic for expressing interspecific differences and adaptability of plants to light levels. Other workers found a ratio of 1.84 to 5.0 (Kwesiga, 1984), 3.37 to 3.84 (Kamaluddin, 1991). The chlorophyll *a:b* ratio obtained for *A. gracilior*, in this experiment, is within the range reported by other worker described above, while that of *J. procera*, particularly at higher nutrient level was higher than most reports, but is close to values report by Kwesiga (1984) for *Triplochiton scleroxylon II* and *Keya senegalensis* when grown under high PPF.

It is generally stated that chloroplasts in shade leaves are larger and richer in chlorophyll *b* relative to chlorophyll *a* than in high light leaves (e.g. Björkman and Holmgren, 1963; Björkman, 1968); and that shade-adapted leaves have a greater number of chloroplasts in the mesophyll cells, adjacent to the upper leaf surface than light-adapted leaves (Goodchild *et al.*, 1972). In a review by Boardman (1977), it was reported that these distinctions are to be well known and have been observed in sun and shade leaves of many species, as well as in single species when grown at low and high light. In addition shade leaves usually have lower contents of soluble protein and a corresponding lower soluble protein to chlorophyll ratio than sun leaves (e.g. Björkman, 1968). Moreover, chloroplasts of shade plants show a greater degree of

grana formation than sun plants. It is believed that grana thylakoids contain a lower chlorophyll *a:b* ratio than do stroma lamellae (e.g. Park and Sane, 1971). Anderson *et al.*, (1973) related the extent of grana formation in shade plant chloroplasts to their total chlorophyll (*a+b*) content and suggested that grana formation may be the means of achieving a higher density of light harvesting pigment assemblies and hence a more efficient collection of light quanta. Higher chlorophyll content per unit leaf area in shade plants is thought to be strongly related to higher quantum efficiency rather than greater absorption of light energy (Björkman, 1968).

Nevertheless, this experiment showed no significant difference in chlorophyll content per unit leaf area with changing light conditions in *J. procera,* nor under high nutrient in *A. gracilior*. However, there was a significant decrease with increasing light in *A. gracilior* in low nutrient conditions, suggesting a higher quantum efficiency. The increasing tendency in chlorophyll *a:b* ratio of those seedlings grown under high nutrient with increasing light is probably related to leaf anatomy. Besides, an increased chlorophyll content with decreasing light on a leaf weight basis confers a significant advantage under low light and severely limiting photosynthetic rate. Therefore, differences in leaf thickness and chlorophyll levels with respect to photon flux levels during growth support the growth data.

6.6.4 Nitrogen content (N)

Since the primary enzyme of CO^2 fixation, RuBP carboxylase, usually contains the major component of leaf nitrogen, nitrogen level may have a profound influence on photosynthetic rate (Herrold, 1980). Tissues with a high concentration of enzymes have higher maintenance cost than tissues that mainly store starch or sugars, and nitrogen content is a crude index of enzyme concentration (cited by Waring and Schlesinger, 1985). When a certain nutrient such as nitrogen is in inadequate supply, construction of photosynthetic enzymes in new foliage is restricted, canopy development slows, and an increasing proportion of carbohydrate moves toward the roots. Additional root growth may increase the uptake of nitrogen and permit shoot growth to continue, but at a lower rate than if nitrogen were supplied in abundance (Ericsson, 1981).

The overall average absolute values obtained in this experiment were 1.0% and 2.2% under low and high nutrient respectively for *A. gracilior*, while the corresponding values for *J. procera* seedlings were 0.9% and 2.1%. There are no data on the leaf N content of Afromontane coniferous species to compare with these values. However, these values compared to the leaf N content of tropical montane and temperate gymnosperm forests, are close to the values reviewed by Jordan (1985).

The species considered in this experiment responded somewhat differently with respect to leaf N content (Fig. 6.17). Values obtained at medium and high light levels were similar for both species, values at the low light treatment for *J. procera* seedlings were significantly lower than for *A. gracilior* seedlings. Also, the leaf N content in *A. gracilior* showed a decreasing trend compared to *J. procera* which had similar N at medium and high light level. In contrast, at higher light levels *J. procera* seedlings demonstrated relatively a higher leaf N with a higher *R* than *A. gracilior* seedlings, which suggests that *J. procera* has a higher light compensation point and is more efficient in using the available N than *A. gracilior* at higher light level. In *A. gracilior* the decreasing leaf N accompanied by relatively decreasing *R*, indicates that *A. gracilior* has a lower light compensation point, and would require higher nutrient with higher light level than *J. procera*.

6.7 Conclusion

Based on the growth analysis, leaf characteristics, leaf chlorophyll and leaf nitrogen content of *J. procera* and *A. gracilior* seedlings in response to light availability and nutrient supply the following similarities emerge:

1. Both species display the qualitative responses to growth at low light that have been identified by other workers as characteristic responses to shade: a positive *R* and *E*, higher specific leaf area, chlorophyll content and chlorophyll *a*:*b* ratio, and thinner leaves; also in allocation of biomass between plant parts: a higher specific stem length, stem weight ratio and a lower root weight ratio.

2. Similarly, the response to high N - supply elicits a shift in the allocation of

biomass between plant parts: higher leaf and stem weight ratios and lower root weight ratios.

3. Both species seem able to survive at photon flux densities as low as 1.99±0.07 mol m^{-2} d^{-1}.

The essential differences between the species are:

1. a higher net assimilation rate at low PPF level in *A. gracilior* than in *J. procera* suggests that *A. gracilior* seedlings are more capable of photosynthesising under low light;

2. a relatively higher chlorophyll content, higher specific leaf area under low PPF and lower chlorophyll *a:b* ratio in *A. gracilior* than *J. procera* suggests that *J. procera* is relatively speaking more of a light demander than *A. gracilior*;

3. the lack of significant differences between treatments in relative stem growth rate under all light conditions sets *J. procera* apart from *A. gracilior*, indicating greater competitive ability in *J. procera* and pointing to better performance in larger gaps or in the understorey, provided nutrient is not a limiting factor, and

4. the low stomatal density and thick leaves coupled with the long tap root occurring in *J. procera* are features which enable the species to maintain more favourable growth conditions in an adverse environment than *A. gracilior*.

Henceforth, it was decided to analyse further the response to shade in controlled environment with constant PPF to investigate the role of R:F-r ratio.

CHAPTER 7

Effect of Red to Far-red Ratio on Seedling Stem Extension Rates

7.1 Introduction

In the work described in the preceding Chapter, no attempt was made to separate the effects of photon flux density from Red:Far-red ratio. A large number of studies on the physiological and ecological significance of spectral quality have documented the capacity of understorey plants to react to dense vegetation with changes in the pattern of morphological development, and much of this reaction is brought about through the change in Red:Far-red ratio (review by Smith, 1986). However, there have been very few studies on the morphogenetic responses of tree seedlings to low R:F-r ratio (Morgan *et al.*, 1983; Kwesiga and Grace, 1986; Warrington *et al.*, 1989; Kamaluddin, 1991). Moreover, there are have been none on the response of the Afromontane coniferous tree seedlings to R:F-r ratio.

In the present Chapter, the effects of a low R:F-r ratio is examined under conditions of constant, and low, photon-flux density. This is to see whether the Afromontane conifers are capable of using the R:F-r ratio as a signal of shade.

The study comprised one long-term and one short-term experiment. In the long-term experiment, seedlings were grown under high, medium and low R:F-r ratio levels, at low photosynthetic photon flux (PPF); in the short-term experiment, stem extension rates were monitored during application of added Far-Red (FR) to the growing internode of seedlings that were growing in white light (WL).

7.2 Material and methods

7.2.1 Long term experiment: Stem extension under varying R:F-r ratios

The 10 week experiment was carried out in a growth cabinet on young seedlings. Each seedling was provided an individual 'shade-cover', constructed in the same manner as described in Section 6.2.2. Three types of filter including chromoid 209

ND, chromoid 422 moss green and the chromoid 116 blue green (Northern Lights, Edinburgh) were used to obtain high, medium and low R:F-r ratios respectively. Silver black scrim (cinelux 270), neutral muslin and nylon fabrics were used where necessary, to obtain the same level of PPF under shade-covers differing in R:F-r ratio. The light transmission and spectral photon flux of the individual filter and other materials used to equilibrate the PPF level were measured in a growth cabinet using the spectroradiometer described in Section 6.2.2 (Fig. 7.1).

The PPF and R:F-r ratio under filters and different layers of silver black scrim, muslin and nylon fabrics were established after several trials to simulate the light conditions observed under the natural forest environment. Initially, the PPF and R:F-r ratio under blue green filter was established. To measure the PPF outside and inside the 'shade-covers' in the growth cabinet, a quantum sensor (Li-190SB, Li-Cor Inc. Lincoln, USA) was used. The R:F-r ratio was measured using a Red:Far-red sensor SKR 110, Skye Instrument, Ltd., Powys Wales, UK). The PPF and R:F-r ratio under shade-covers are given in Table 7.1. Light spectra were measured at the internode level within each shade-cover with a glass fibre optic light guide connected to the spectroradiometer (Fig. 7.2).

Table 7.1: The materials used for the 'shade-cover' and their light environment in the growth cabinet.

Filter materials used	PPF ±SE (μmol m^{-2} s^{-1})	R/FR ratio (±SE)
1 layer 209ND filter, 1 layer silver black scrim, 1 layer muslin, 4 layers nylon fabrics	38.7±0.7	1.27±0.02
1 layer 422 moss green filter, 1 layer silver black scrim, 4 layers nylon fabrics	38.5±0.8	0.51±0.04
1 layer blue green filter	38.6±0.7	0.09± 0.01

i) Plant materials and experimental design

The seedlings for this experiment were raised in a similar method to those described in Section 6.2.1. The potted seedlings were brought from the glasshouse and were placed on the experimental bench in a growth cabinet for a week under white light.

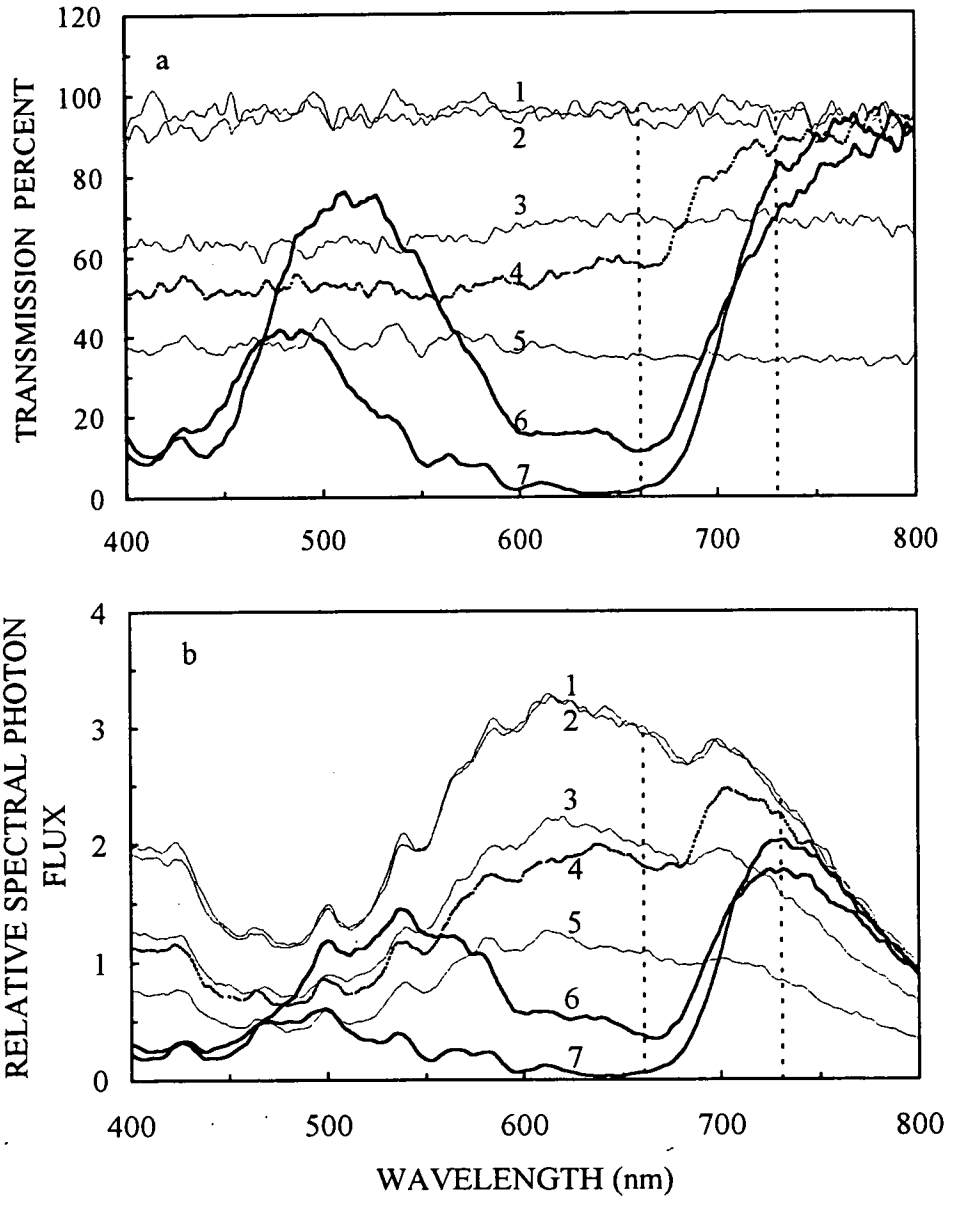

Figure 7.1: (a): Transmission percent and (b): relative spectral photon flux of 'shade-cover' materials used during the growth of *J. procera* and *A. gracilior* seedlings under low, medium and high Red:Far-red ratio treatment in a growth cabinet. 1: open experimental bench condition; 2: nylon fabric; 3: muslin; 4: 209 neutral density filter; 5: silver black scrim; 6: 422 moss green filter, and 7: 116 blue green filter. The dotted vertical line indicate the relevant transmission % and relative spectral density required to calculate R:F-r ratio.

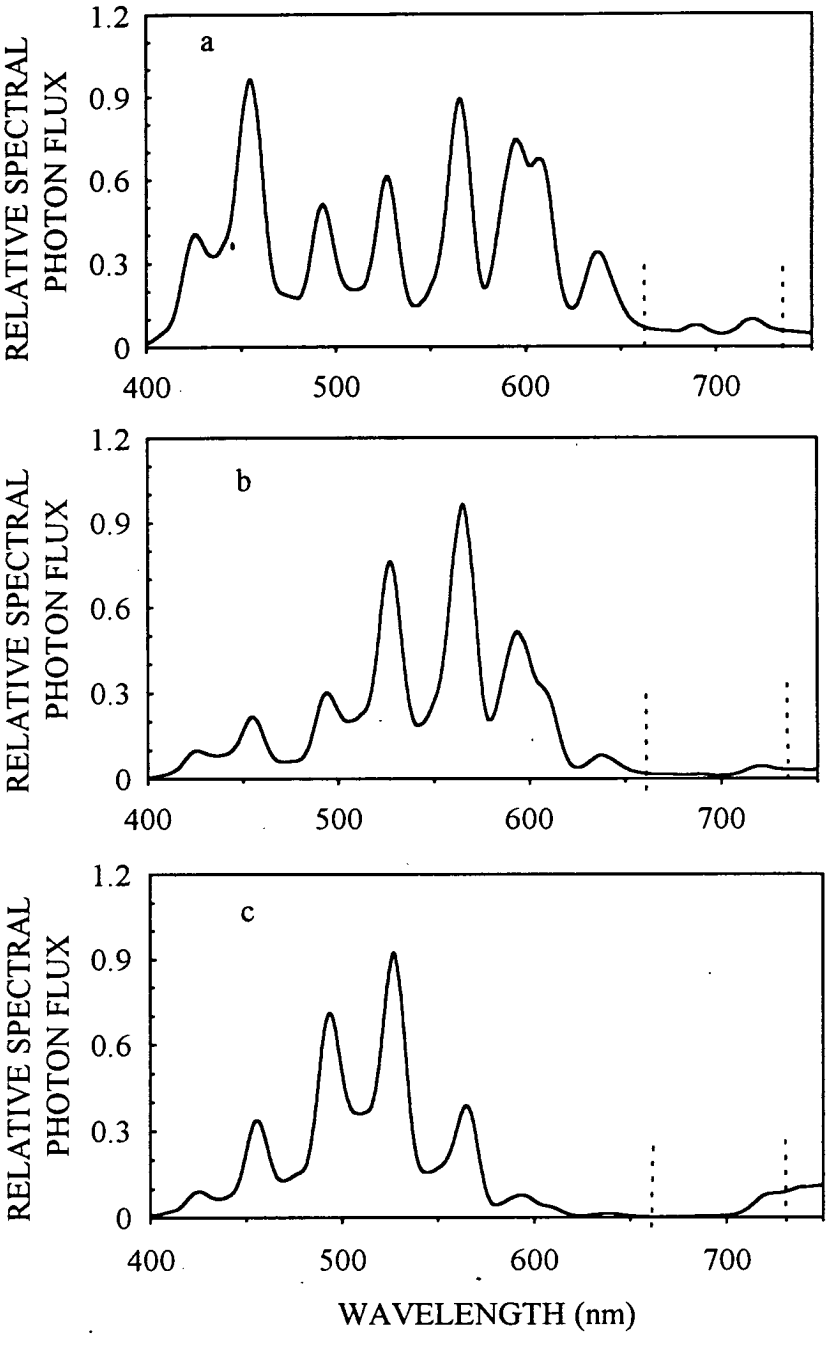

Figure 7.2: Relative spectral photon flux inside 'shade-covers' during the growth of *J. procera* and *A. gracilior* seedlings in a growth cabinet. a: 1 layer 209 neutral density filter, 1 layer silver black scrim, 1 layer muslin and 4 layers of nylon fabric; high R:F-r ratio (1.27); b: 1 layer 422 moss green filter, 1 layer silver black scrim and 4 layers nylon fabric, medium R:F-r ratio (0.51); c: 1 layer blue green filter; low R:F-ratio (0.09). The dotted vertical lines indicate the relevant Red and Far-red wavelenghts.

The seedlings' age at the start of experiment was about 3 weeks and their heights ranged from 2.8 to 4.9 cm. The seedlings were sorted into groups of 8 relatively similar height groups. The three R:F-r ratio levels including high, medium and low, were applied each with 8 seedlings of each species, and set up with 8 replications in a randomised block design on an experimental bench in a growth room.

ii) Nutrition

The seedlings were fed with a nutrient solution prepared as described in Section 6.2.4. The nutrient solution was diluted with de-ionised water to provide 30 mg l^{-1} of N, and about 50 ml of nutrient solution was applied once a day.

iii) Other growth conditions

The PPF on the bench was 470±18.5 μmol m^{-2} s^{-1}, with a 12 h photoperiod. The lights used in the growth cabinet were 400-W metal halide lamps (kolorarc MBIF/H, Thorn Lighting, London, UK) supplemented with 60-W incandescent bulbs to enrich the far-red. The day and night temperatures were 25 and 20 °C respectively. The relative humidity was about 70 %.

iv) Data collection and analysis

Eight representative seedlings were harvested at the beginning of the experiment. Leaf area and dry weight were measured and recorded. Seedling height was recorded weekly throughout the experiment. After 10 weeks of growth under treatment the seedlings were harvested. Stem length, leaf area and the dry weight of the different plant organs of each seedling were measured, recorded and growth analysis was done in a similar manner as described in Section 6.3.1.

Relative biomass growth rate (R), net assimilation rate (E) stem extension rate (H), leaf area ratio (F) stem weight ratio (s), specific leaf area (S), Specific stem length (L), leaf weight ratio (w) and root weight ratio (r) were determined. The variation in each parameter was investigated by analysis of variance (ANOVA).

7.2.2 Short-term experiment: Stem extension rates by irradiating seedling internode with added Far-red

i) Plant materials and growth conditions

The seedlings of both species were raised in a glasshouse in the same manner as those seedlings used in the preceding section. But, the seeds were sown at an interval of 2 weeks to get more or less similar age/size seedlings for the experiment. The seedlings were brought from the glasshouse after one week of growth to the growth cabinet and were grown under white light (WL) for 2 to 3 weeks before the experiment. The PPF in the growth cabinet was reduced to 120 μmol m^{-2} s^{-1} at the plant level by reducing the number of lamps. The photoperiod was 12 h. The day and night temperature were 25 and 20 °C respectively. The relative humidity was 70%. The plants were supplied with similar nutrient solution to that used in Section 6.2.4, applied as and when necessary before the experiment. During the experiment each seedling was fed from a tray by seepage from below.

ii) Recording extension rate

Extension rates were monitored using a linear voltage displacement transducer (LVDT, type DFG/5, ± 5.0 mm stroke, RS Components, Corby, UK) as illustrated in Fig. 7.3. The LVDT had a sensitivity of 54.34 mV mm^{-1}. The LVDT was mounted in an adjustable supporting stand, with the armature running freely through the barrel. Plants and transducers were coupled by a balance and cotton thread tied around the first internode just below the primary leaf node. The thread was passed through a small pulley wheel. Two LVDTs were used allowing one seedling of each species to be monitored simultaneously. The outputs from the LVDTs were logged using a Delta-T logger. The extension rates were sampled every 5 s and recorded over 5-min interval. In order to avoid vibration noises, anti-vibration pads were provided under the supporting stand. The growth cabinet was closed during measurement and recorded outside the growth cabinet in the next room. The two transducers were monitored for vibration noises for 28.3 hours and showed mean 'drift' rates of -0.0009±0.016 μm min^{-1} and -0.0004±0.017 μm min^{-1}.

The experiment involved recording the extension rate under two conditions lasting for 72 hours (3 days) for each seedling. These include: (1): under continuous white light (WL) as a control, and (2): in a sequence of 'WL-FR-WL' representing

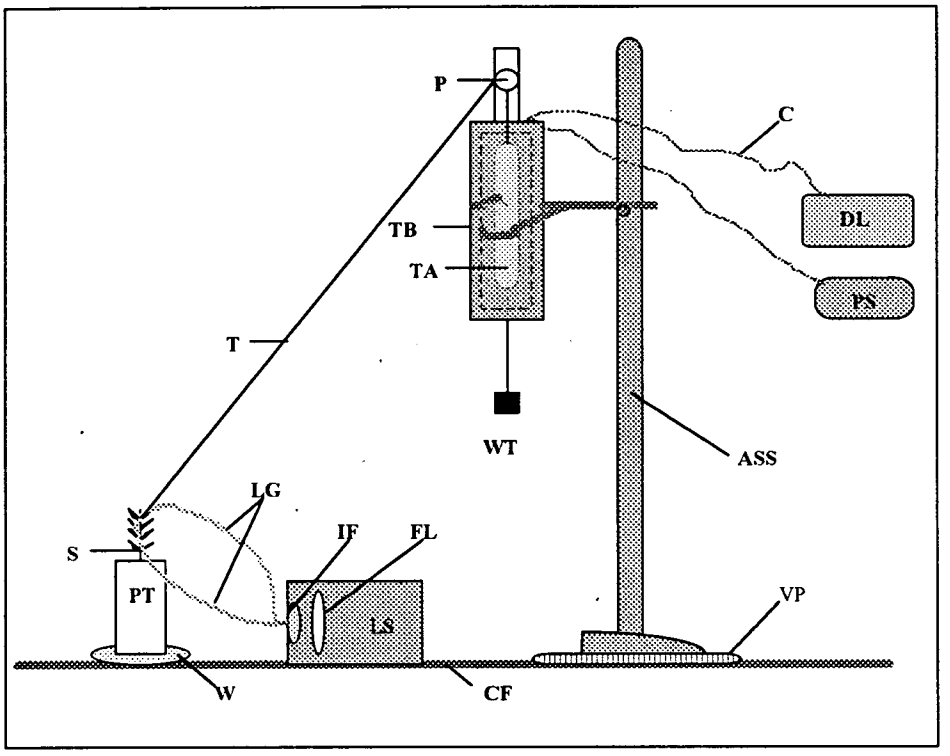

Figure 7.3: Diagrammatic representation of a linear voltage displacement transducer (LVDT) apparatus used during the measurement of stem extension rates of *J. procera* and *A. gracilior* seedlings. S: seedling; PT: seedling pot tube; W: Nutrient solution in a germination tray; LG: light guide; IF: interface filter; FL: focusing lens; LS: light source; T: cotton thread; P: pulley; TB: transducer body; TA: transducer armature; WT: weight; ASS: adjustable supporting stand; VP: anti-vibration pad; DL: Delta-T logger; PS: power supply; C: cable, and CF: concrete floor.

open-shade-open of the forest conditions for 24 hours for each phase. Six seedlings of each species were subjected to condition one, and twelve seedlings of each species to condition two.

ii) Light sources

The light source was a slide projector (LUX 150S, Fortt, Ltd., Tonbridge, Kent, UK) having a tungsten- halogen bulb, with light focused by a lens onto an interference filter (Fig. 7.3). Supplementary FR was supplied to the seedling's terminal internode via a fibre-optic light guide mounted with an interference filter (FR max = 730 nm, 25 mm diameter, Glen Spectra, Middlesex, UK). The whole system assembly was cooled by an electric fan within the system. The fluence rates and spectral photon distribution of the background white-light (WL) source and FR fibre-optic probes were measured using a spectroradiometer. The FR radiation at about 35 μmol m^{-2} s^{-1} in a background WL of 120 μmol m^{-2} s^{-1} resulted in a drop of R:F-r ratio from 1.75 of the WL to 0.12 (Fig. 7.4).

7.3 Results

7.3.1 Growth characteristics of seedlings under contrasting R:F-r ratios

i) Stem extension

The seedlings of both *J. procera* and *A. gracilior* showed a similar pattern of stem extension in response to R:F-r ratio treatments (Fig. 7.5). Stem extension growth increased with decreasing R:F-r ratio. The stem extension of seedlings grown under low R:F-r ratio was significantly higher than those grown under medium or high R:F-red ratios. On the other hand, there was no significant different between the medium and high R:F-r ratios.

The data may also be expressed as rates (Fig. 7.6). There was a tendency for the rate to decline after 5 - 6 weeks, especially in the low R:F-r plants.

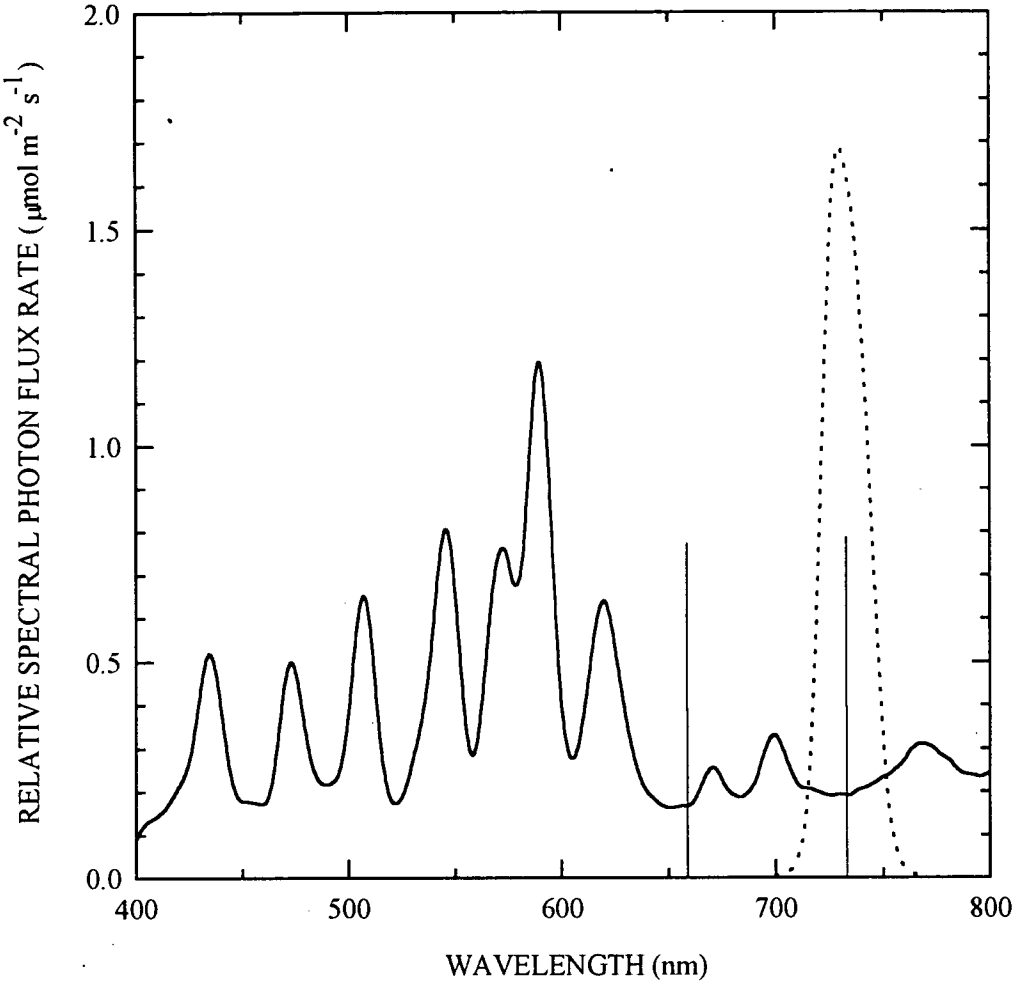

Figure 7.4: Relative spectral photon fluence rate of white light (solid line) and added Far-Red (dotted line) used during stem extension of *J. procera* and *A. gracilior*. Far-red radiation of about 35 μmol m^{-2} s^{-1} (730 ± 25 nm) in a background white light (WL) of 120 μmol m^{-2} s^{-1} resulted in a drop of R:F-r ratio from 1.75 to 0.12. The short vertical lines indicate the relevant Red and Far-red wavelengths.

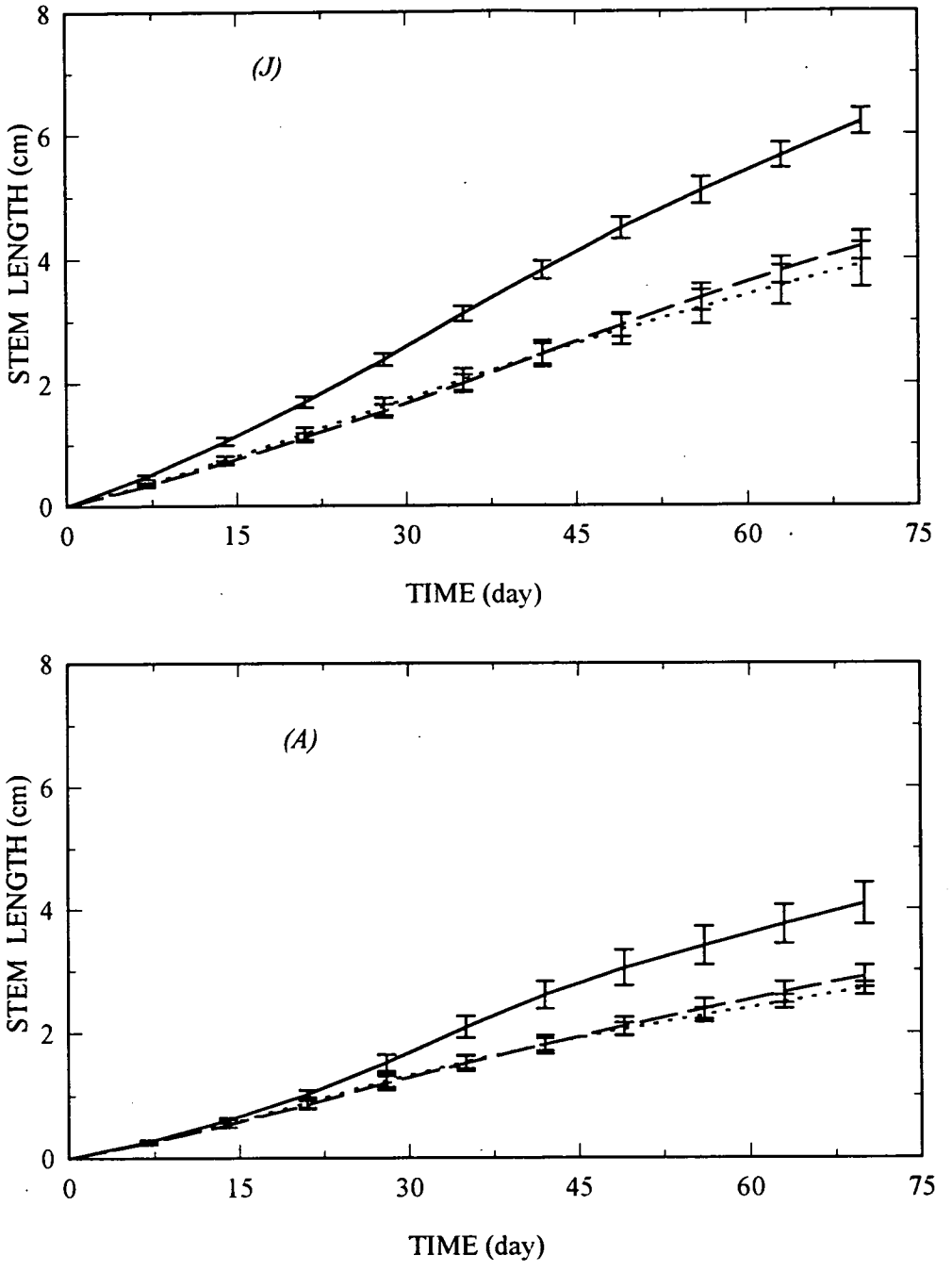

Figure 7.5: Stem extension of *J. procera (J)* and *A. gracilior (A)* seedlings grown under different Red:Far-red ratio treatments for 10 weeks in a growth cabinet. High R:F-r ratio, 1.27: (dotted line); medium R:F-r ratio, 0.51: (dashed line), and low R:F-r ratio, 0.09: (solid line). Each datum point is the mean of 8 seedlings; vertical bar indicates standard error of the mean.

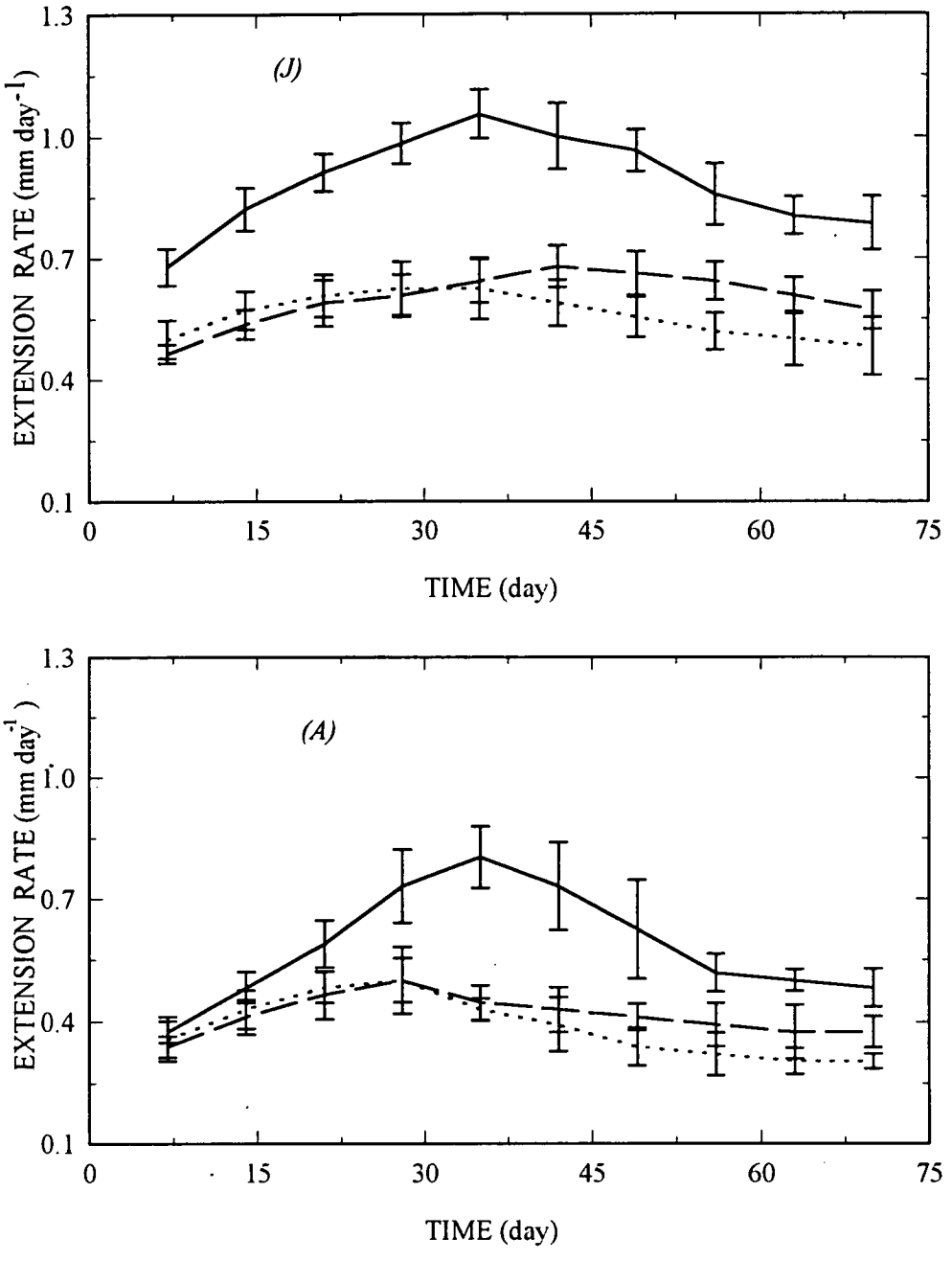

Figure 7.6: Weekly stem extension rate of *J. procera (J)* and *A. gracilior (A)* seedlings grown under varying Red:Far-red ratio treatments for 10 weeks in a growth cabinet. High R:F-r ratio: (dotted line); medium R:F-r ratio: (dashed line), and low R:F-r ratio: (solid line). Other particulars are as described in Figure 7.5.

ii) Other morphological responses

The morphogenetic adjustments in response to contrasting R:F-r ratios are summarised in Tables 7.2 and 7.3. In *J. procera*, low R:F-r ratio induced a significantly higher *s* and significantly lower *w* than the high R:F-r ratio but no other response was detected. Seedlings subjected to medium R:F-r ratio treatments took the intermediate position in these morphological responses. In *A. gracilior* there were additional responses: specific leaf area increased at low R:F-r, and specific stem length declined.

Table 7.2: Growth characteristics of *J. procera* seedlings grown under high, medium and low (1.27, 0.51 and 0.09) R:F-r ratios for 10 weeks in a growth cabinet. Duncan's multiple range test. Mean ±SE, n = 8 seedlings. Means preceded by the same letter are not significantly different from each other at $P = 0.05$.

Variables	Red:Far red ratio			Value of	
	High	Medium	Low	*F*	*P*
Biomass relative growth rate, *R* (mg^{-1} g^{-1} wk^{-1})	a0.057 (0.005)	a0.060 (0.003)	a0.058 (0.005)	0.79	0.466
Net assimilation rate, *E* (mg cm^{-2} wk^{-1})	a1.119 (0.037)	a1.259 (0.057)	a1.220 (0.044)	0.91	0.426
Leaf area ratio, *F* (cm^2 mg^{-1})	a0.066 (0.010)	a0.067 (0.008)	a0.066 (0.010)	0.02	0.984
Specific leaf area, *S* (cm^2 mg^{-1})	a0.123 (0.014)	a0.127 (0.016)	a0.134 (0.022)	0.75	0.483
Specific stem length, *L* (cm mg^{-1})	a0.172 (0.024)	a0.189 (0.031)	a0.166 (0.032)	1.21	0.317
Stem weight ratio, *s* (mg mg^{-1})	b0.201 (0.037)	ab0.209 (0.020)	a0.245 (0.035)	3.85	0.038
Leaf weight ratio, *w* (mg mg^{-1})	a0.541 (0.049)	ab0.526 (0.027)	b0.491 (0.017)	4.06	0.032
Root weight ratio, *r* (mg mg^{-1})	a0.259 (0.061)	a0.265 (0.026)	a0.265 (0.036)	0.05	0.955

Table 7.3: Growth characteristics of *A. gracilior* seedlings grown under high, medium and low (1.27, 0.51 and 0.09) R:F-r ratios for 10 weeks in a growth cabinet. Duncan's multiple range test. Mean ±SE, n = 8 seedlings. Means preceded by the same letter(s) are not significantly different from each other at $P = 0.05$.

Variables	Red:Far red ratio			Value of	
	High	Medium	Low	*F*	*P*
Biomass relative growth rate, *R* (mg^{-1} g^{-1} wk^{-1})	a0.109 (0.010)	a0.106 (0.009)	a0.109 (0.011)	0.27	0.768
Net assimilation rate, *E* (mg cm^{-2} wk^{-1})	a1.380 (0.098)	a1.383 (0.094)	a1.382 (0.132)	0.23	0.800
Leaf area ratio, *F* (cm^2 mg^{-1})	a0.119 (0.004)	a0.115 (0.003)	a0.119 (0.008)	0.14	0.866
Specific leaf area, *S* (cm^2 mg^{-1})	b0.200 (0.005)	b0.205 (0.006)	a0.233 (0.016)	4.05	0.041
Specific stem length, *L* (cm mg^{-1})	a208 (10.95)	a207 (3.93)	b178 (9.10)	4.73	0.027
Stem weight ratio, *s* (mg mg^{-1})	b0.190 (0.006)	ab0.209 (0.011)	a0.267 (0.003)	27.09	0.000
Leaf weight ratio, *w* (mg mg^{-1})	a0.594 (0.013)	b0.578 (0.014)	c0.511 (0.004)	13.52	0.001
Root weight ratio, *r* (mg mg^{-1})	a0.216 (0.011)	a0.213 (0.005)	a0.222 (0.005)	0.39	0.685

7.3.2 Seedling stem extension rate in response to added Far-red

Fig. 7.7 illustrates the short-term extension rates obtained by adding FR to the growing internode of both *J. procera* and *A. gracilior* seedlings under a background of equilibrated WL. These data represent the average responses of 12 individual seedlings calculated as 30-minute running means. Under all cases a very high fluctuation of extension rate was recorded. On average, however, the application of FR resulted in a higher extension rate compared to WL_1 and WL_2 (Table 7.4). The difference was significant in *A. gracilior* seedlings but not in *J. procera*.

Table 7.4: Stem extension rates ($\mu m\ min^{-1}$) of *J. procera* and *A. gracilior* seedlings before FR (WL_1), during FR and after FR (WL_2) treatment. Means±SE of 12 seedlings. Means preceded by the same letter for each species are not significantly different from each other at ($P = 0.05$) (ANOVA and Duncan's multiple range test). Paired *t-test* was used to test the significance of differences between the treatment means of the two species. For all-test; d.f. = 11.

Variable	Mean±SE *J. procera*	Mean±SE *A. gracilior*	*t* value	*P* *(2-tail)*
Rate before FR treatment (WL_1)	a0.42±0.06	b0.35±0.04	3.57	0.004
Rate during FR treatment	a0.56±0.04	a0.49±0.03	4.00	0.002
Rate after FR treatment (WL_2)	a0.44±0.05	c0.26±0.02	6.02	0.000
F-statistics (*P*-value)	2.22(0.125)	13.69(0.000)		

The mean stem extension of seedlings grown for 72 hrs under continuous WL and under alternate WL_1-FR-WL_2 is shown in Fig. 7.8. On average, the extension rate of *A. gracilior* seedlings was 0.33 $\mu m\ min^{-1}$ under WL, while it was 0.43 $\mu m\ min^{-1}$ for *J. procera* seedlings. These values were significantly lower than the overall growth of WL_1-FR-WL_2 (*J. procera*: $t = 28.374$, $P = 0.000$; *A. gracilior*: $t = 26$, $P = 0.000$; d.f. 12).

7.4 Discussion

7.4.1 Evaluation of the light environment

In these experiments, levels of PPF as low as those measured in the forest understorey of Arba-gugu reported were achieved (see Section 3.4.1). The high and medium R:F-r ratio treatments used in experiment one (Table 7.1), were comparable to the highest and lowest R:F-ratios of the *J. procera-A. gracilior* 60 cm above the ground in Arba-gugu. On the other hand, the R:F-r ratio values of 0.09 used for the lowest R:F-r ratio treatment in Experiment one, and 0.12 for Experiment two were actually much lower than those measured in the forest. The values used in these experiments are within the range of R:F-ratios reported by Vázques-Yánes and Smith (1982) in the rainforest of Los Tuxtlas, Mexico. They found a R:F-ratio ranging from 0.3 to less

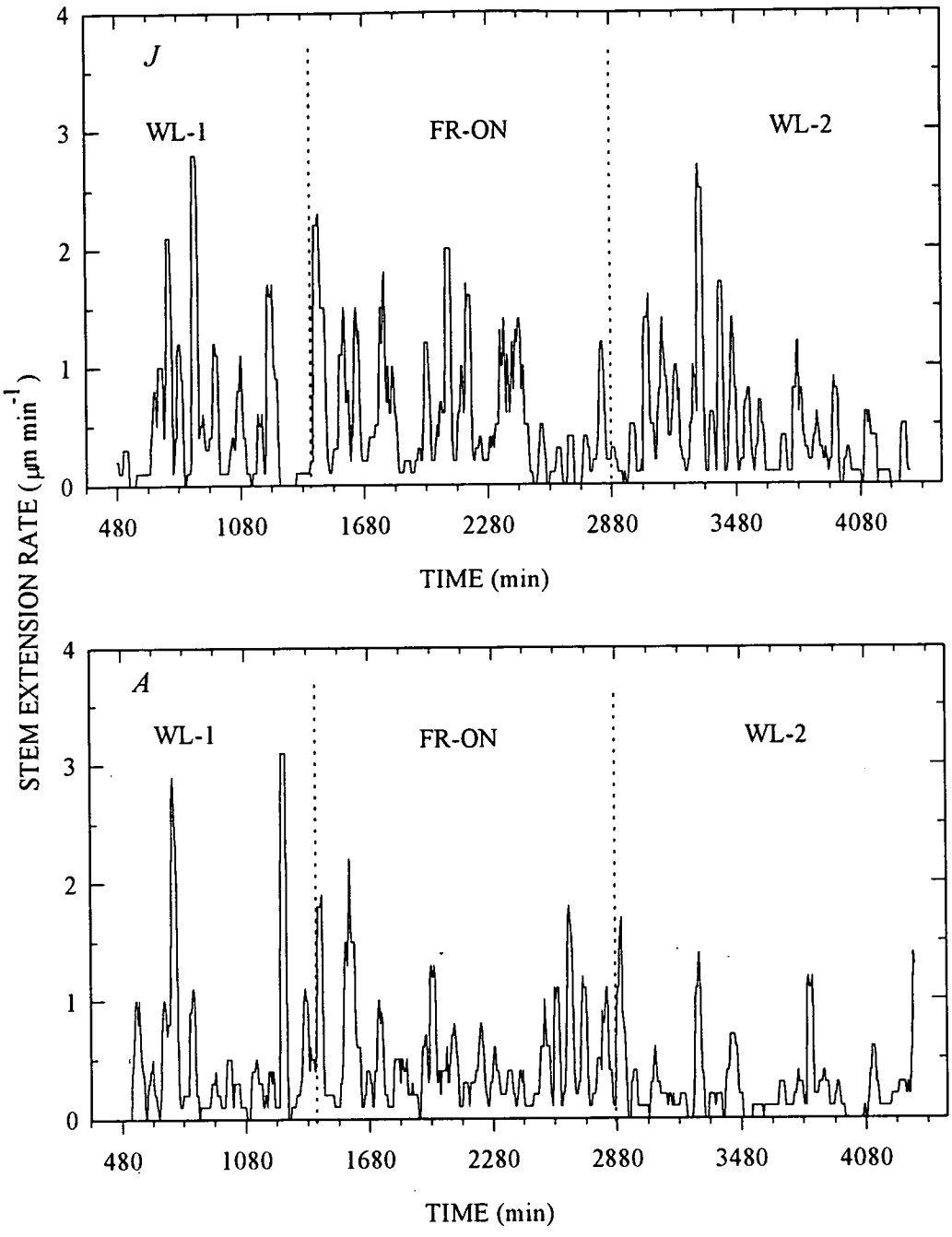

Figure 7.7: The effect of irradiating the first internode of seedlings with added FR on stem extension rate. *J. procera* (*J*) and *A. gracilior* (*A*). Added FR was irradiated (FR-ON) for 24 hrs to a background light of 120 μmol m^{-2} s^{-1} and R:F-r ratio of 0.12 from fibre-optic light-guides. The stem extension was monitored for a total of 72 hrs in a sequence of white light (WL_1), added FR (FR-ON) and white light (WL_2) for 24 hrs each. Thirty minutes running mean of 12 seedlings. Area between two dotted vertical lines indicates the period of FR treatment (FR-ON).

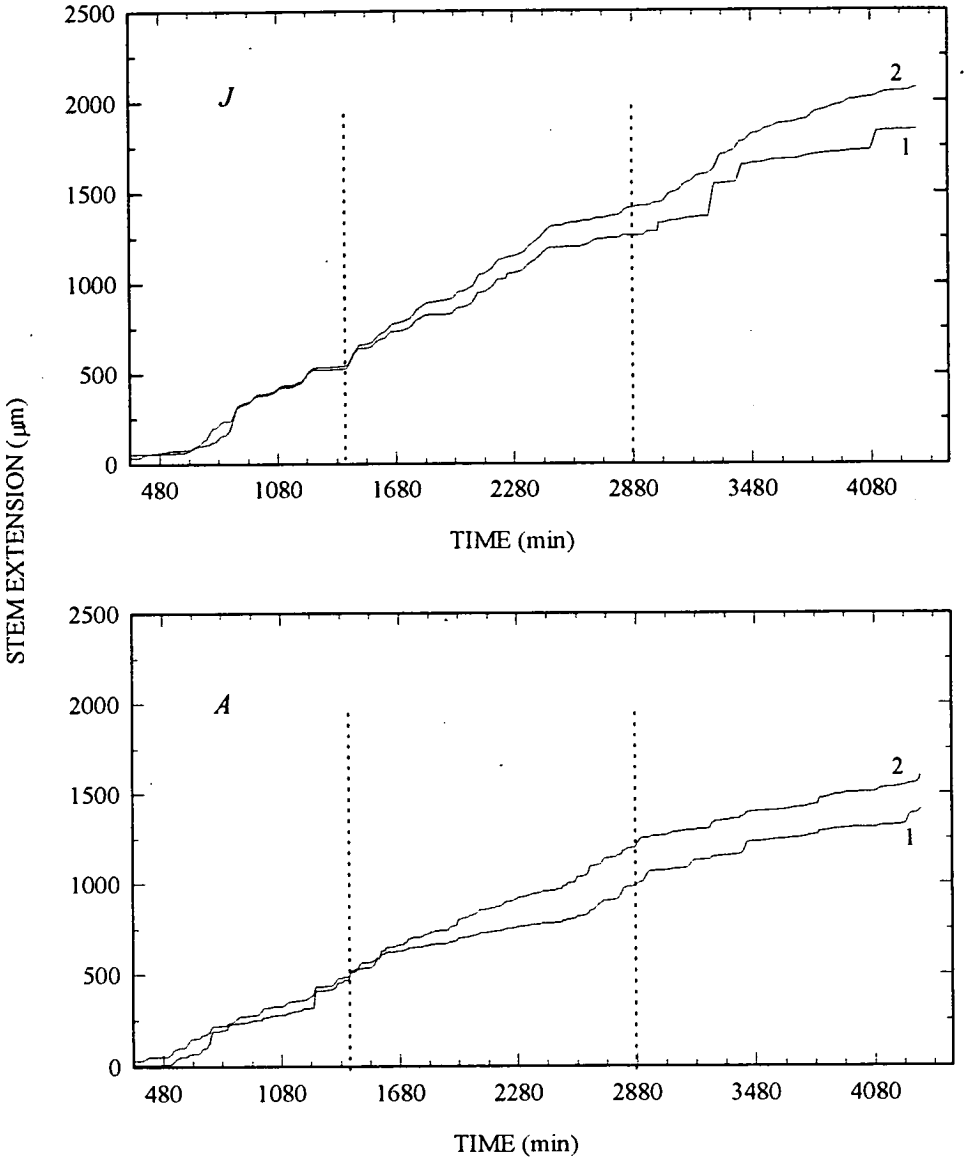

Figure 7.8: Comparison of seedlings stem extension of *J. procera* (*J*) and *A. gracilior* (*A*). 1: under continuous white light (control); 2: alternate treatments of white light-added FR-white light for 24 hrs each. The stem extension of the seedlings was monitored for 72 hrs under each treatment and the first 8 hrs observation is excluded in each case. Mean of 12 seedlings. Area between two dotted vertical lines refer to line number 2 and indicates the period of FR treatment.

than 0.02 in dense part of the forest using a field spectroradiometer. Hence, the light levels and the low R:F-r ratios values used in both experiments are comparable with those found in relatively dense vegetation, where competition for the light resource is particularly intense, thus helping to evaluate the response of the species to such low R:F-r ratios.

7.4.2 Effect of R:F-r ratios

In general, seedlings of both *J. procera* and *A. gracilior* showed an increase in stem extension with decreasing R:F-r ratios (Fig. 7.5; 7.6). However, the increase was not significant in both species under the medium and high R:F-r ratios. Under a low R:F-r ratio value of 0.09, both species displayed a large increase in stem extension (Fig. 7.5; 7.6). This significant response of the long-term observation under low R:F-r ratio is supported by the higher stem extension rates, when the terminal internode was irradiated with added Far-red (Fig. 7.7; 7.8 and Table 7.4). R:F-r ratio is directly related to the phytochrome photoequilibrium, Pfr/P (review by Smith, 1986). Low R:F-r ratios reduce the Pfr/P (Morgan and Smith, 1976; Child and Smith, 1987). There are no comparable data on Afromontane tree species. However, the responses of stem extension to low R:F-r obtained in the present experiment are similar to those obtained by Kamaluddin (1991) for pioneer *Anthocephalus chinensis* Rich. ex Walp from Asia.

The reduction in stem extension rates after 5 weeks of growth in both species (Fig. 7.7) could be interpreted as the demand for more light as the seedlings grow older. This is because at low light levels, photosynthetic limitations become important, reducing the capacity of the plant to react to low R:F-r ratio by accelerated extension rates (cited by Child and Smith, 1987). Shade avoiding plants respond to shade by extreme elongation of the internodes, until the photosynthetic structures are carried into the open, or until the stored food reserves are used up (review by Smith, 1986). Thus, both species investigated in this study, had responded by stem elongation initially to the low light using their stored food, which later declined with declining storage reserves. The seedlings used in these experiments had all been grown for about 3 weeks under WL and thus may have been fully de-etiolated. The hypocotyl had completed its period of growth and all seedling extension during the experiments was due to the first internode. On the other hand, the period during which the hypocotyl extends and the cotyledon leaf expansion becomes photosynthetic, is a crucial transition as far as phytochrome is concerned in a natural environment. Hence,

once the environment for seed germination is facilitated for natural or artificial regeneration (Chapters Four and Five), the seedlings have the capacity to compete with the herbaceous growth.

Abrupt extension rates following the addition of FR has been reported for a large number of herbaceous plants by several workers (e.g. Morgan and Smith, 1976; Morgan *et al.*, 1980; Lecharny and Jacques, 1982) and for *Anthocephalus* a tropical tree species (Kamaluddin, 1991). However, the present study has failed to demonstrate such abrupt stem extension rates in either species.

Since each set of observations is derived from a single plant, normal biological variability becomes a serious problem. Accumulating data from several plants in order to reduce variability by the standard averaging procedures can, conversely, lead to important details being hidden or lost. This is particularly true for an attempts to define precisely the timing of events which may not occur in complete synchrony in all the experimental individuals. Also, the accurate determination of the lag periods of the seedlings was difficult because of normal biological variability within the experimental individuals and time-base resolution (Child and Smith, 1987) and particularly, the naturally slow growth of the species in this case.

The response to reduced R:F-r ratio, of a higher s and low w (both species Table 7.2; 7.3) is presumably a shift in allocation from leaf to stem associated with the increased stem extension (Corré, 1983a; review by Smith, 1986). The significantly high s, significantly low w in *J. procera* (Table 7.2) indicate that the increased stem extension under low R:F-r ratio was more the result of a change in dry matter allocation from leaf to stem than that of a reduction in stem thickness. This is an important difference between the effects of light quality and light quantity, in that L mainly depends on the amount of energy fixed by the plants, thus, it depends more on the quantity of light than on light quality (Smith, 1981). The absence of significance difference in S between treatments in *J. procera* agrees with the findings reported by other workers (Morgan and Smith, 1981; Kamaluddin, 1991). In contrast, *A. gracilior* seedlings grown under low R:F-r ratio had a significantly high S (Table 7.3). Similar results with respect to increase with a reduction in R:F-r ratios were reported by Kwesiga and Grace (1986) for the pioneer tree seedlings of *Terminalia ivorensis*.

CHAPTER 8

General Discussion and Conclusions

8.1 Evaluation of the project

In general, the results from both the natural and the controlled environments agree with the patterns and trends mentioned in the literature. The study of the forest understorey environment was helpful in understanding the light, air temperature and soil moisture experienced by the understorey shrubs, tree saplings and seedlings, especially the herbaceous perennials. The field regeneration experiment was particularly helpful in assessing the effects of logging waste disposal, disturbing the ground vegetation and the forest floor compared to just canopy opening to enhance the regeneration and establishment particularly of *Juniperus procera*.

Controlled environment conditions permit comparative studies without the problem of high variability and the confounding effect of environmental factors associated with field studies (Whitehead *et al.*, 1981). The controlled environment experiments provided important insight into the viability of the forest soil seedbank, behaviour of seeds to different light conditions and seed pre-germination treatments, and the physiological responses of seedlings to light quantity and quality, and nutrient regimes. The better understanding of the performance of the seedlings and comparison of the species when grown at different light and nutrient conditions in a controlled environment was also invaluable as these were inadequately understood in field conditions.

Although it has been possible to simulate two main features of forest shade, namely the reduction in photon flux with or without an appropriate reduction in the R:F-r ratio, the large variations in energy that occur as a result of sunflecks (Chapter 3) were more difficult to simulate. This is particularly important when considering rapid fluctuations of the environment, in particular sunflecks, wind and rain. Sunflecks are extremely important for plants growing under shade since a substantial amount of photosynthesis is obtained from them, and dynamic responses of the plant may be very important (Pearcy *et al.*, 1985). This suggests that values obtained under fixed

controlled, conditions should be used with caution when simulating field conditions or comparing with field data.

8.2 Field studies/experiments

8.2.1 The forest environment

The large differences in canopy gap fraction of the *J. procera* and *A. gracilior* forest would be expected to create to substantially different light climates. The distribution of radiation, particularly direct radiation, under the rather typical *J. procera*-dominated forest examined was quite heterogeneous. This indicates that, especially in this type of open-canopied forests, the distinction of "gaps" and "non-gaps" appears to be an oversimplification, because gaps of different sizes exist throughout the forest. The results of this study must also be understood in the context of a long history of disturbance, including grazing by cattle.

The light environment in the understorey is brighter and less spectrally altered than in humid, broadleaved forests. Typically PPF values and percentage of daily totals were 5-10 times higher than broadleaved forests reported from the tropics (Pearcy, 1983; Chazdon and Fetcher, 1984), but the percentage PPF transmissions are similar to the temperate coniferous forests reported by other workers (Vales and Bunnell, 1988; Canham *et al.*, 1990). The values of site factors (diffuse and direct), potential sunflecks per day estimated from hemispherical photographs and contribution of sunflecks to measured PPF confirm that the forest under investigation is a high light environment. The R:F-r ratio is like temperate and boreal coniferous forests (e.g. Federer and Tanner, 1966), rather than broadleaved forests (e.g. Stoutesdijk, 1972b; Turnbull and Yates, 1993).

In tropical rainforests the seedlings and saplings of many tree species exhibit rapid acceleration in growth only after falling trees create gaps that allow more light into the understorey. However, if the forest is open-canopied as in the forest of the present study, competition from ground vegetation may impose new limitations. Root competition or competition from herbaceous plants has been shown to be more important in determining tree seedling growth in the understorey of an English oak woodland than light (Jarvis, 1963).

Furthermore, both open condition and the forest understorey is characterized by high day and low night air temperatures with adequate moisture which favours the germination of seeds of many species. Hence, the high light with uniform spectral distribution, fairly small daily air temperature variation with adequate soil moisture content experienced in this forest would be an advantage to the growth of understorey shrubs, tree saplings and seedlings, especially the herbaceous perennials.

8.2.2 Regeneration microsites and the soil seedbank

Evaluation of *J. procera* and *A. gracilior* regeneration microsites on sites with different disturbance histories indicate remarkable similarities in light transmission, forb and shrub cover (Table 4.1, 4.2). But the undisturbed understorey site had a significantly greater litter depth and higher percentage grass cover. Furthermore, the grass and forb cover was also much taller than at the disturbed sites. Hence, it seems that germination of seedlings found on disturbed sites was not much influenced by light availability. But the most open and severely disturbed site had higher and more uniformly distributed regeneration of *J. procera*.

Examination of the soil seedbank of the forest understorey revealed not less than 9 viable *J. procera* seeds m^{-2}. Thus, the nature of the forest environment and evaluation of the regeneration microsites suggests that viable seeds of *J. procera* found in the undisturbed forest floor and soil seed bank could have germinated if the ideal conditions had been met. Hence, the 6 to 8 times greater persistent litter depth and the high percentage cover of tall grasses found in the undisturbed forest understorey compared to the disturbed regeneration sites might have hindered the germination and establishment of regeneration of *J. procera* seeds. Grass is often reported to be very effective in preventing subsequent tree establishment. Some grasses, once established, adversely affect germination and establishment of trees seedlings either mechanically or by competing for moisture and nutrients (McNiel, 1955; Leyton, 1955; Robertson, 1976). Carvell (1979) reports that the only species that can effectively establish themselves on thick leaf litter are those with large seeds (cited by Smith, 1986). This is because the big seeds may be buried beneath the litter by rodents or by litterfall and yet have enough stored material to grow back up through the litter compared to small seeds. Crawley (1986) also claims that the larger the seed, the less disturbance is necessary for successful establishment compared to small seeded species. Hence, large seeded species like *A. gracilior* may germinate

more readily on thick litter than relatively small seeded species like *J. procera* which may require disturbance of the forest floor to expose the mineral soil.

8.2.3 The influence of clearcutting and ground preparation on regeneration

The previous sections summarized the forest environment, regeneration microsites of disturbed sites and the status of the soil seedbank. The initial response that occurred in connection with forest harvesting and alternative post harvesting site treatments are discussed in this section. Clearcutting with ground preparation that exposes the mineral soil seems the most practical silvicultural method for regeneration *J. procera*. The large amounts of residue left after logging not only leave the areas unsightly and create fire hazards, but impede forest management activities. Of particular concern initially is managing the residues so as to encourage regeneration and growth of the new forest. In this study three post-logging and cultivation treatments were tested.

Combined treatment of clearcutting in strips with seeding from adjacent stands and exposure of the mineral soil through mechanical scarification or controlled burning have resulted in adequate regeneration of *J. procera*, whilst *A. gracilior* did not respond to this treatment. The germination was significantly high in the burning treatment for *J. procera* and lowest for *A. gracilior*. The percentage germination of *J. procera* was further increased by cultivation in all treatments (control, raking and burning), whereas, cultivation brought a further reduction in the germination of *A. gracilior*.

Natural regeneration potential for *J. procera* varied significantly by treatment type. Clearcutting alone resulted in poor natural regeneration. The natural seedlings obtained in this study represent about 400 ha^{-1} for clearcutting alone (control), 7,600 ha^{-1} in combination with mechanical scarification, and 12,000 ha^{-1} in combination with control burning. In contrast, no natural regeneration of *A. gracilior* appeared in any of the treatments. This complete lack of natural regeneration of *A. gracilior* is probably due to lack of seed dispersal. An evaluation of the experimental site showed that *J. procera* exhibits an extensive seed dispersal, whereas *A. gracilior* seems to lack the capacity for it. While detailed investigation was not carried out the presence of *J. procera* seeds and new germinating seedlings embedded in bird droppings, and the harbouring of black-winged lovebirds (*Agaponnis taranta*)

in the *J. procera* trees indicate that this birds may play an important role in the process of natural regeneration particularly as a seed dispersal agent.

It is clear from the result that clearcutting alone (control plots) would require supplemental planting or seeding to restock the site adequately. However, since the artificial regeneration (sown seeds) of both species was poor on the clear cut treatment, sowing more seed to assure adequate regeneration again would be impractical because of limited and costly seed supplies. Hence, planting seems the only alternative to restock the site after clearcutting and where seeding from adjacent stands is not possible.

In addition to surviving at different rates, as shown (Chapter 4) differences in height were apparent within 19 months where *J. procera* seedlings grew most on burning treatment plots and least on the mechanical scarification and control plots. Many individual factors or combinations thereof probably contribute to differences in seedling response. But nutrients are often felt to be a major cause of differential tree responses on areas treated with some of the residue disposal methods used in this study. Burning is likely to bring about increased levels of potassium, calcium, magnesium, and nitrates and may have contributed to the superior growth of the regeneration that developed as a result of natural or artificial seeding. In contrast, in the mechanical scarification treatment the removal of all logging waste, litter and ground vegetation gave poor growth. This is assumed to be due to the poor nutrient content of the exposed mineral soil. But the least seedling response was in the control plots with the greatest percentage of organic matter. This might be due to the fact that much of the nitrogen may have been "tied up" in the organic matter and as a result unavailable to the seedlings even though present.

Moreover, the measurement of light transmission under the herb growth, which covered the experiment plot following the treatment, also confirms that light does not seem to have any immediate effect on germination in this experiment. However, at least in the burning plot, the more rapid development and higher seedling density means that competition between plants will begin sooner, which may result in higher mortality rates, an effect which may be enhanced by competition with other herbaceous growth.

It is important to mention the difficulty experienced in this study to ignite and achieve effective fire treatment due to the high moisture content of the fuel material and wet

weather condition. The experience reported by Norum (1981) based on about 100 broadcast fires made in experimental studies in larch/Douglas-fir forests, both on clear cuts and under standing timber in the Northern Rocky Mountains, indicates that a safe and practical range of moisture contents is between 10% and 17% for small diameter fuels. He found that, below 10% moisture content the fire behaviour and fire intensity becomes increasingly extreme, and becomes problematic to control. On the other hand, above 17% the fire becomes extremely difficult to ignite and an effective fire treatment is less likely. Hence, timing of prescribed fires to achieve satisfactory site preparation for silvicultural purposes is critical. Fires during rainy seasons usually burn over a wet logging waste, wet ground vegetation and wet thick litter layer and therefore are unsuccessful in baring mineral soil. Following dry seasons fires remove all the fuel material and expose adequate mineral soil for forest regeneration. Even then, it seems that fuels and litter must dry for several days following significant precipitation. Conditions under which fire can be effective in Arba-gugu forest to substantially reduce the fuel materials usually occur during May and early June and late October to January, the months when precipitation is low (see Appendix 2.1).

The intensity of fire is also important for the proportion of mineral soils exposed and for the stocking of tree seedlings. This should be decided based on not only on the moisture content and thickness of the fuel material but also on habitat type. According to DeByle (1981) high-intensity fires over a dry fuel material on mesic sites expose a high proportion of mineral soil, resulting in a dense overstocking of tree seedlings following good seed crop. Hence, on mesic sites moderate-intensity fires can generate enough heat to consume most of the dry fuel and prepare adequate seedbed, while fires of similar intensity on thicker and wetter fuel material will expose less mineral soil resulting in poor regeneration. Controlled burning conducted in the present study was high-intensity fire due to a thick litter layer, green fuel materials with wet weather conditions. This would have had a significant effect on the soil under the burned piles of logging waste, ground vegetation and thick litter layer and would have killed any roots and propagules within it. This is evidenced from the post-fire vegetation which was quite different from the pre-fire vegetation and control plots.

Timing of ripening and dispersal of the seed as well as its abundance must be considered when using controlled burning as a silvicultural tool. At the regeneration experiment area, main seed crops of *J. procera* were dispersed during late November. This was about one month later than the seed dispersal on nearby lower slopes and valley bottoms any where in the Arba-gugu area. Controlled burning can, therefore,

be accomplished on the upper slopes through mid October before seed is dispersed. Elsewhere the dispersed seed will be destroyed by fires later than about September and regeneration of the treated site has to wait for the next seed crop. This demonstrates the difference in the timing of ripening and dispersal of *J. procera* seed between habitat and suggests the importance of timing of controlled burning with seed dispersal.

The germination and seedling survival data indicate that the method used to dispose of wood residues, and treatment of the ground vegetation and the leaf litter following clearcutting in *J. procera-A. gracilior* forest, clearly affects subsequent regeneration. This holds true for both germination, survival and initial development of *J. procera*. Apparently the logging waste, ground vegetation and the litter layer must be removed from any microsite on which *J. procera* natural regeneration is expected in sites similar to Sanka-Meda. How much of the overall area needs to be bared to mineral soil is a question that can be answered only on a site-by-site basis, taking into account the expected seed crops and all mortality between the time of seed dispersal and satisfactory seedling establishment. Also, the extent to which the differential effects of the site treatment will continue over time is not yet clear. Schmidt (1982) cites various authors who did similar studies, on *Larix occidentalis* in USA and showed that effects of seedbed treatments affecting seedlings and saplings development may continue for 15 to 20 years.

8.3 Controlled experiments

8.3.1 Germination responses to light regimes and different seed pre-germination treatments

Various factors regulate the germination of seeds in their natural habitat, some of which are internal, whereas others are external environmental factors. Any of these can determine whether a given seed will germinate in a certain place or not. However, the result demonstrated in the laboratory of the existence of a regulating mechanism is not proof of its operation under natural conditions. To prove this and to show that the plant derives some definite advantage from a given regulatory mechanism is much more difficult. The only advantage about which one may justifiably speak is where some special mode of germination has survival value for the species in a specific environment. The ecological conditions prevailing in a given habitat will affect

germination, the determining factor being probably the micro-climatic conditions prevailing in the immediate vicinity of the seed. Normally, seeds are shed so as to fall either on soil or leaf litter. Possibly the soil may consist of leaf litter or partially decomposed matter which may contain substances inhibiting germination. Seeds in their natural habitat interact with other plants and with animals. The interaction with other plants may be due to inhibitors, stimulators or modification of the microhabitat. Animals may effect germination behaviour by seed softening in the digestive tract or by distribution to other habitats. A range of management practices can be an important contributor to changes in the environment. As shown above, fire can also affect germination behaviour.

Light is one of the environmental factors which may regulate germination. Seeds requiring light will not germinate when they are buried under soil or leaf litter, but will germinate when they fall on the soil surface. Seeds of the same genus may be light-requiring (positive-photoblastic) or light-inhibited (negative- photoblastic). In some cases different varieties of the same species may be light-requiring or light-indifferent, for example *Lactuca sativa*. Light requirement is frequently associated with small seeds, which are supposed to contain rather small amounts of reserve materials, so that it might be advantageous for them to germinate under conditions where photosynthesis occurs very soon after germination. The preferred combination of favourable light, moisture, temperature and suitable substrate for germination and seedling establishment apparently is rare in nature.

Chapter 5 has demonstrated some of these external factors which may play a role in regulating germination. A range of pre-germination treatments failed to significantly improve the percentage germination of *J. procera*, whilst only cutting the seed coat at the radical end significantly improved the percentage germination of *A. gracilior*. Heat pre-germination treatment decreased germination in *J. procera*, while totally inhibited germination of *A. gracilior*. Sulphuric acid and hot water pre-germination treatments resulted in nil germination for both species. *J. procera* seed germination showed indifferent behaviour to the presence or absence of light, while dark treatment significantly improved percentage germination of *A. gracilior*.

The result, therefore, reveals considerable interspecific differences with respect to germination strategy. Seeds of *A. gracilior* exhibited seed coat-imposed dormancy. Hard seed coat in known to occur in many plant families and usually cause dormancy by making the seed coat impermeable to water, to gases or it may mechanically

constrain the embryo (Mayer and Poljakoff-Mayber, 1989). This was not absolute however, but seems to strongly restrict the range of environmental conditions that allow their germination. This seed coat dormancy was broken by cutting the seed coat at the radical end. In this case, *J. procera* hardly showed any seed coat-imposed dormancy. In nature, most seeds become permeable to water when the seed coat is broken down or punctured by mechanical abrasion, microbial attack, passage through the digestive tract of animals or exposure to alternating high and low temperatures which, by expanding and contracting the seed coat, cause it to crack.

It is interesting to note that *J. procera* seeds germinated readily in darkness but do not appear to be incorporated into the flora of the undisturbed forest floor. The germination of *J. procera* seeds under a range of simulated canopy light and complete darkness in a glasshouse confirms the results of the field observation (Chapter 4), and shows that in its natural environment, factors other than light quantity or quality is controlling germination. It is likely that the seeds of *J. procera* may germinate and rapidly die if the stored food reserve is exhausted before the root system reaches the mineral soil. The observations made here on the characteristics of the light control of seed germination are essentially preliminary and would repay more detailed investigation under field condition. The study of the optical properties of the seed coat may help understanding how the seeds of both species can germinate under dark moist conditions.

It could be argued that once germination has occurred, the process of regeneration is complete and subsequent performance can be regarded as no different to any crop, no matter how established. However, this view cannot be accepted for two main reasons. Firstly, in the case of artificial regeneration with seedlings from nursery stock, such seedlings will have already passed through the most vulnerable period by the time it is planted out and will therefore be free from many of the adverse conditions faced in the field (e.g. Brown *et al.*, 1988). Secondly, conditions suitable for germination are not those most efficacious for optimal development (e.g. McNeill, 1962) and hence forest management will have to be concerned with this new optimal growth requirement. This is discussed in the next section particularly from the point view of light availability and nutrient supply.

8.3.2 Response to light regime and nutrient supply

The experiments on light regime have confirmed that many of the conclusions made in the literature regarding the response to shade, based on observations of herbaceous crops, temperate and tropical trees, generally hold for Afromontane coniferous trees. It has, moreover, been possible to separate the effects of a reduced photon flux *per se* from those of a reduced photon flux coupled with a low Red:Far-red ratio.

A high level of seedling mortality in the early stage after germination has been widely reported (e.g. Noble and Ronco, 1978; Alexander, 1984). Several factors strongly influence initial seedling survival. Following logging, if herbs, shrubs, and trees all become established in the first year, as they often do, herbs will dominate the initial stages of succession because they grow and develop most rapidly (DeByle, 1981). By definition herbs die back to the ground annually, and this growth pattern, often brings sudden changes in cover from year to year caused by changing climate conditions. As a result the tree seedlings experience different light levels which may affect their development. Particularly, vegetation shading increases the mortality of those germinants coming at later years after original site disturbance (e.g. McNeill and Thompson, 1982).

Moreover, conditions for optimal development change as the seedlings grow. Not only does the nutrient status of the site become more important, but the requirements for light alter. Nutrients may not be much of a problem for survival in early growth. Nevertheless, on degraded soils, for instance, such as plots of the raking treatment in this study (where the logging residue, the ground vegetation, the leaf litter and the unincorporated organic matter have been removed), nitrogen and mineral deficiency are likely to restrict growth. This condition is enhanced when there is competition with ground vegetation (McNeill, 1955). Some authors also report reduced levels of nitrogen, phosphorus and potassium on scalped plots, though they conclude that the levels of exchangeable potassium and total nitrogen were not affected (Zasada and Grigal, 1978 in Binkley, 1984). On the other hand, under conditions where the logging residues are not removed, the nutrients locked up in the debris would eventually become available to the seedlings, and nitrogen availability is 7 to 20 times greater on clearcut sites compared to uncut stands. Hence, if regeneration is to be successful, it is necessary to understand the responses of seedlings to light availability and nutrient supply.

In the present study, seedlings adjusted to shade in several ways. One of the most important of these seemed to be the increase in specific leaf area that occurred when leaves had been formed at low photon flux. It was through this increase in specific leaf area that the leaf area ratio was increased, hence counteracting the low net assimilation rates that inevitably occurred in low PPF.

In both species, there was an increase in specific leaf area (S) in seedlings grown at low PPF (Chapter 6). An increase S combined with an almost equal leaf weight ratio (s) led to an increased leaf area ratio (F), and this relative increase in leaf area compensated, at least partially, for a lower photosynthesis per unit leaf area under low PPF. In this way, F made a significant contribution in maintaining a positive relative growth rate (R) under low PPF.

Shade tolerant species are able to grow under low PPF because they are able to maintain a positive net assimilation rate (E), and hence a positive R under light-limiting understorey habitats. Seedlings of both *J. procera* and *A. gracilior* had maintained a positive E under low PPF. Both species seem able to survive at photon flux densities as low as 2±0.07 mol d^{-1} or 46.3 μmol s^{-1} m^{-2}. However, a larger increase in S in *A. gracilior* under low PPF and hence a larger F resulted in higher net assimilation rate (E) compared to *J. procera*. As a consequence, *A. gracilior* maintained a higher R under low PPF compared to *J. procera*. These results are in accordance with most other studies that have been identified by other workers as characteristic responses to shade (e.g. Oberbauer and Strain 1985; Pompa and Bongers, 1988). Though seedlings of both species show an increase in F in response to shade, the magnitude of this is generally much higher in the seedlings of pioneers (e.g. Pompa and Bongers, 1988). In this respect, seedlings of *J. procera* behaved like pioneer species. Relatively higher net assimilation rate in *A. gracilior* seedlings grown under low PPF indicates that *A. gracilior* was more shade tolerant than *J. procera*.

Leaf anatomy showed that leaves of both species produced under low PPF were thinner, had only a rudimentary palisade layer and loosely arranged mesophyll tissues (Fig. 6.11). This means a lower amount of photosynthetically active mass per unit leaf area. Lower maximum photosynthetic rates in thinner low-light leaves have been observed for non-pioneer and pioneer forest tree seedlings of *Flindersia brayleyana* (Thompson *et al.*, 1988) and *Nauclea diderrichii* (Riddoch *et al.*, 1991a) respectively. Also, the leaves of both species are amphistomatous and leaves developed at low PPF displayed lower stomatal density. As a consequence their maximum rates of

photosynthesis were lower than when the leaves had been grown in higher PPF conditions as evidenced from the net assimilation rate (Fig. 6.8).

J. procera seedlings manifested similar height growth under all light conditions, and faster height growth than *A. gracilior* under lower PPFs, which confirms the height growth data obtained from field experiment (Chapter 4). Hence, *J. procera* has an early advantage to compete with rapidly germinating herbaceous growth indicating a better establishment.

Both species had a higher chlorophyll content on a weight basis under low PPF. But this effect is more pronounced in *A. gracilior* than in *J. procera*. Similarly, the response to high N - supply elicits a shift in the allocation of biomass between plant parts: higher leaf and stem weight ratios and a lower root weight ratio.

To rank *Juniperus procera* and *Afrocarpus gracilior* in terms of their level of tolerance as an indication to the distribution in the forest understorey and in clearings, based on the present study, their ecological characteristics and physiological responses appear as follows: The essential differences between the species are:

1. a higher net assimilation rate at low PPF level in *A. gracilior* than in *A. procera* suggests that *A. gracilior* seedlings are more capable of photosynthesising under low light;

2. a relatively higher chlorophyll content, higher specific leaf area, higher leaf nitrogen content under low PPF and generally lower chlorophyll *a:b* ratio in *A. gracilior* than *J. procera* suggests that *J. procera* is relatively speaking a greater light demander than *A. gracilior*;

3. the lack of significant differences between treatments in relative stem growth rate under all light conditions sets *J. procera* apart from *A. gracilior*, indicating greater competitive ability in *J. procera* and pointing to better performance in larger gaps or in the understorey, provided nutrient is not a limiting factor;

4. the lower stomatal density and thicker leaves coupled with long tap root occurring in *J. procera* compared with *A. gracilior* are features which

enable the species to maintain a more favourable conditions in an adverse environment compared to *A. gracilior*.

Other adjustments to shade involving stem extension and development were species-dependant varying with the ecological characteristics of the tree. These will be considered in the next section.

8.3.3 Response to Red:Far-red ratio

Seedlings of both *J. procera* and *A. gracilior* showed several growth responses to low R:F-r ratio values of 0.09 (Chapter 7). The main effect of a reduction in R:F-r ratio was a significant increase in stem extension rate, when grown under constant low PPF with contrasting R:F-r ratios for 10 weeks. This long-term effect of a low R:F-r ratio on stem extension rate was in agreement with short-term observations. Significantly higher stem extension rates in *J. procera* seedlings were also observed (a) when the internodes were subjected to low R:F-r ratios as well as (b) when the terminal internode was irradiated with added far-red radiation to lower the R:F-r ratio at the internode level. This higher stem extension rate as a result of a low R:F-r ratios is an inverse linear function of Pfr/P of photoreceptor phytochrome (Morgan and Smith, 1976). This linearity has been found for a wide range of herbaceous species (review by Smith, 1986) and for older materials of *Pinus radiata* (Warrington *et al.*, 1989).

With an increase in stem extension rate, dry matter allocation to stem was significantly increased resulting in a higher stem weight ratio, with a simultaneous reduction in leaf weight ratio. This indicates that the increased stem extension was at the expense of the development of leaf. Further, the increased stem extension, particularly in *J. procera* under low R:F-r ratio was more the result of change in dry matter allocation between plant organs than that of a reduction in stem thickness as is evident from a non-significant specific stem length (*L*) (Table 7.3). This also confirms the important difference between the effects of light quality and light quantity, in that specific stem length mainly depends on the amount of energy fixed by the plants and thus depends more on the quantity of light than on light quality (Smith, 1981). These results are consistent with those reported for herbaceous plants (review by Smith, 1986), and confirm that pioneer tree seedlings are not different from herbaceous species from open habitats in response to a low R:F-r ratio. Increased stem weight ratio with concomitant increase in stem extension rate has also been found for the material of *Pinus radiata* (Warrington *et al.*, 1989) and pioneer tree species

Anthocephalus chinensis (Kamaluddin, 1991) when grown under low PPF and a low R:F-r ratio. In contrast to these results, Kwesiga and Grace (1986) found differential growth response between pioneer and climax species. In their experiment, specific leaf area was enhanced under low R:F-r ratio in pioneer species *Terminalia ivorensis*, whereas it was largely unaffected in climax species *Khaya senegalensis*. In *A. gracilior*, specific leaf area was enhanced and specific stem length declined under low R:F-r ratio.

In this experiment, the increase in stem extension was not significant in both species under the medium (0.51) and high (1.27) R:F-r ratio treatments, which were the lowest and highest R:F-r ratio levels measured in the forest understorey and open conditions in the natural environment. Hence, the PPF levels and the low R:F-r ratio values used in both long-term (Table 7.1) and short-term experiments are comparable with those found in a relatively dense herbaceous habitats found by other workers (Vázques-Yánes and Smith, 1982), where competition for light resource is particularly intense.

The results on the effects of low R:F-r ratio, suggest that seedlings of *J. procera* are relatively more plastic in their responses, and hence, *J. procera* is a responding pioneer species more than *A. gracilior*.

8.4 Implications

8.4.1 Ecological implications

A physiological explanation relating growth, survival and distribution of light demanding and shade tolerating Afromontane species cannot be advanced on the basis of simple, short term duration, controlled environment experiments, such as described here. The influence of shade on seeds was investigated only on two species. Besides, extrapolating the results from investigations in controlled environments to field conditions is fraught with difficulty. Whereas in controlled environments some variables can be controlled and one of particular interest investigated; under field conditions, the variables fluctuate and interact together and influence the plant in a complicated way. Moreover, artificially simulated environments may fail to represent important features of field conditions. Nevertheless, the data from these experiments

contribute to an understanding of gross ecological phenomena such as initial response to light and nutrient supply.

8.4.2 Silvicultural/management implications

The present understanding of plant ecology and physiology has been gained mainly from studies conducted in temperate regions and a few studies of tropical plants. When an equivalent amount of research has been done, hopefully including the Afromontane forest vegetation, it will be necessary to appraise the present trial-and-error Afromontane forest management. For instance the concept of 'desirable' and 'undesirable' species has led to selective creaming of these forests, and future demands of such wood will have to be met through forest plantations now in their infancy, or through some form of enrichment planting. The causes of poor natural regeneration and its control need further research on a large scale to establish the factors involved such as vegetational shade-light and its influence on seed germination and seedlings development under field condition. Thus, knowledge of species physiological responses in a given environment will enable us to establish a basis of management that takes into account the whole forest instead of a few 'desirable' species. Moreover, it should ultimately be possible to predict the outcome of any attempt to divert succession in a desirable path, as in artificial regeneration.

Appreciation of differences in species physiological responses in a particular forest location is an important silvicultural tool in forest management. Rational utilization to meet a given objective of management requires knowledge of factors limiting productivity such as nutrient availability, temperature and moisture stress. Shade has been implicated as one of the main causes of poor natural regeneration. Natural regeneration is accounted for by the number of surviving seedlings and the number of seeds involved may be enormous. Physiological responses like those reported here, coupled with a knowledge of photon flux and its spectral distribution, may enable controlled thinning to achieve regeneration. Possibly, mismanagement like that reported in Chapters 1 and 2 may be averted. However, at present only a few studies have been carried out in this respect, and control of natural regeneration remains one of the most serious constraints in understanding the reproduction of Afromontane forests.

In selectively logged forests, increasing the proportion of the so called desirable species such as during enrichment planting/artificial regeneration requires knowledge of species responses to vegetational shade-light. In an attempt to get natural regeneration of *J. procera* and *A. gracilior* forest, opening the canopy by selective logging to increase the light levels reaching naturally regenerating seedlings on the forest floor, may result in further increase of undesirable pioneer weed species. This would not have happened if growth responses to small and large canopy gaps were known at the time.

For some purposes, it is necessary to manage the forest to produce low density, fast growing, short lived pioneer species. A case like this would be averted if enrichment planting is carried out in large gaps and clearings. Fast growing pioneer species cannot withstand shade but can grow fast in the open; thereafter they can be utilized in the large gaps where they encounter intraspecific competition, enhanced apical dominance and increased leaf area index to shade other species. These responses have been utilized in plantation monocultures: the lowermost branches die continuously as a result of shading (self pruning) and trees develop relatively short narrow crowns. However, in un-even-aged mixed stands and natural forests, small seedlings and younger trees may grow slowly, depending on spacing density, and may be suppressed or overtopped by large, older and other fast growing trees. This fact is important in choice of species based on growth rates and other physiological attributes.

Although, the interaction of seedbed condition, seed availability, and environmental factors may restrict the regeneration of conifers following prescribed fires, any of these alone may limit regeneration to unacceptable levels.

In summary, the information provided by this study suggests that regeneration of *J. procera* should involve more complete disturbance of the forest floor to remove the barrier both for rooting and seedling emergence above ground. Clearcutting in narrow strips is indicated to provide an adequate seed supply and site preparation which exposes the mineral soil particularly control burning so as to provide other favourable conditions for seedling establishment. In contrast, this operation is likely to inhibit the regeneration of *A. gracilior*. A silvicultural systems that will provide minimum soil disturbance may encourage its regeneration. But, more research under field conditions will be required to get an appropriate answer.

The complexity and duration of forest production require an equally complex analysis of alternatives and estimated impacts due to changes in the production process. Forest management consists of a sequence of highly interdependent silvicultural practices or activities. Thus changes in practice at one stage may affect later options and the outcome of subsequent stages. Forest managers, therefore, need to anticipate the effect of practices within the scope of the management sequence and to modify or mitigate particular cultural practices as required, based on the ecology and physiological response of the species. To ignore these in managing a forest is to court disaster.

8.5 Suggestions for further research

It is important to attempt more research into the ecology, physiology and silvicultural systems of Afromontane forest ecosystems. There is a certain urgency for developing a framework for managing this vital but disappearing resource not only for the values described in Chapter 2, but also for the value of *J. procera* and *A. gracilior* forests in reducing soil erosion on steep slopes or ameliorating the climate in semi-arid areas and for multiple forest use such as grazing. These research priorities include:

1. Field trials, conducted in a similar way to those described in the present work, on a large scale and under different environmental conditions.

2. Similar site preparations as those conducted in this study, but under standing timber of the forest.

3. Studies of the survival rate of natural seedlings on a variety of seedbed types over a period of years: this is important since there will be high levels of seedling mortality in the early years after germination due to competition for light or other factors.

4. Studies of stem extension of herbs found in the *Juniperus-Afrocarpus* forest understorey in response to R:F-r ratio, which is an area where ecological work is badly needed to provide an insight into the competition between tree seedlings and forest weeds.

5. If the light level during sunflecks exceeds light saturation for a long period, photoinhibition of photosynthesis may occur, and responses of seedlings to sunflecks may be an important area of investigation. This is particularly important to understand the response of the species, particularly when cultural practices such as release operations from weeds are to be undertaken following regeneration. Field studies parallel to laboratory investigation may yield a good understanding.

6. Light dynamics and nutrient availability are not the only factors influencing the regeneration of a forest. Clearly, there are many other factors such as seed dispersal, moisture relation, and allelopathy are also important, and hence, an urgent need for more research relevant to forest management.

7. There are many examples of low-input agroforestry systems in various ecological regions of the tropic where tree species are deliberately mixed with crops (agroforestry) or animals (silvo-pasture) or both (agro-silvo-pasture) in order to derive maximum economic and ecological benefits (e.g. review by Nair, 1992). But the extremely site-specific nature of agroforestry, conditioned by biophysical and sociocultural characteristics, poses serious difficulties in developing precise recommendations of wider applicability. Hence it is difficult to extrapolate agroforestry systems from one place to another. Thus research trials of those scientific methods of agroforestry and silvo-pasture that are already being used elsewhere are suggested in the *J. procera* and *A. gracilior* forest ecosystems to minimize the damage from over grazing and encroachment from cultivation.

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APPENDICES

Appendix 2.1: Summary of mean monthly rainfall data (mm) for Guna and Aseko meteorological stations located about 15 km west and 10 km east of the centre of Arba-gugu forest at an altitude of 2600 m and 2100 m respectively. Mean values for 1989 and 1990.

	Meteorological station		
Month	Guna	Aseko	Mean
January	11.4	12.5	12.0
February	145.2	91.4	118.3
March	90.6	123.4	106.8
April	170.4	271.0	220.7
May	54.0	57.0	55.5
June	20.3	55.0	37.7
July	175.8	175.9	175.8
August	153.9	151.3	152.6
September	159.2	208.8	184.0
October	42.8	52.9	47.9
November	12.6	15.0	13.8
December	45.7	76.0	60.9
Total (mm)	1082	1290	1186

Source : Guna Meteorological Station, Arba-gugu (unpublished data).

Appendix 3.1: Daily total observed photosynthetic photon flux (PPF) and PPF-Fraction of the open (large clearing) and shade (understorey) of *J. procera* and *A. gracilior* forest stand at Arba-gugu during March/April 1991 (mol m^{-2} d^{-1}).

Location	Julian day	PPF open	PPF shade	PPF fraction
1	76	39.27	5.42	0.138
	77	39.41	5.62	0.143
	78	39.34	5.53	0.141
Gap edge	81	39.11	19.45	0.497
	82	22.32	12.77	0.572
	83	7.05	3.38	0.479
2	85	23.27	3.42	0.147
	86	28.52	2.83	0.099
	87	17.56	2.73	0.155
3	89	32.13	3.39	0.105
	90	25.83	3.27	0.127
	91	18.49	2.26	0.122
	92	26.56	3.69	0.139
4	93	29.12	9.79	0.336
	94	39.84	14.44	0.362
	95	39.45	13.85	0.351
5	101	24.81	3.12	0.126
	102	28.48	3.29	0.115
	103	21.46	3.53	0.165
6	105	33.41	1.63	0.049
	106	43.34	0.94	0.022
	107	43.27	1.15	0.027
7	109	28.18	5.15	0.183
	110	22.81	4.14	0.182
	111	29.60	6.39	0.216
	112	28.04	3.94	0.141

Appendix 3.2: Descriptive statistics for predicted diffuse, direct and global radiation (mol m^{-2} d^{-1}) computed from hemispherical photographs of Arba-gugu *J. procera* and *A. gracilior* forest for every quarter month from 21st December to 21st June. Calculation was done from 1 solar track for December and from 4 solar tracks for other months. a) Annual means for each of the 7 plots. b) Monthly means for all plots together. Gap edge location is not included.

i) DIRECT RADIATION:

a) Yearly means for each locations:

Location	Mean	SEM	Median	Min	Max
Calculated	46.88	1.501	48.96	41.21	50.94
1	4.0	0.53	3.8	2.5	6.3
3	3.9	1.02	2.9	1.0	7.4
4	3.0	0.39	2.7	1.5	4.4
5	6.2	1.17	6.4	2.5	11.1
6	5.7	1.02	5.6	1.8	9.9
7	4.1	1.37	1.9	1.0	9.2
8	9.7	1.74	9.2	5.2	18.1
Mean	5.2	0.85	4.1	3.0	9.7

b) Monthly means for locations:

Month:	Mean	SEM	Median	Min	Max
December	5.2	0.93	5.2	2.5	9.2
January	5.3	0.91	5.5	2.6	8.2
February	5.3	0.75	6.2	2.5	7.1
March	5.0	1.39	3.8	1.4	11.1
April	4.0	1.38	2.5	1.0	9.9
May	5.9	1.63	5.1	1.0	13.0
June	5.8	2.17	4.7	1.0	18.1
Mean	5.2	0.23	5.3	4.0	5.9

Appendix 3.2: continued

ii) DIFFUSE RADIATION:

a) Yearly means for each locations:

Location	Mean	SEM	Median	Min	Max
Calc	8.91	0.219	9.23	8.09	9.49
1	0.77	0.019	0.79	0.70	0.82
3	0.61	0.015	0.63	0.55	0.65
4	0.61	0.015	0.63	0.55	0.65
5	1.27	0.031	1.32	1.16	1.36
6	0.87	0.021	0.90	0.79	0.93
7	0.79	0.019	0.82	0.72	0.84
8	1.49	0.037	1.54	1.35	1.59
Mean	0.92	0.128	0.79	0.61	1.49

b) Monthly means for locations:

Month	Mean	SEM	Median	Min	Max
December	0.83	0.116	0.72	0.55	1.35
January	0.84	0.118	0.73	0.56	1.37
February	0.89	0.125	0.77	0.59	1.45
March	0.95	0.132	0.82	0.63	1.54
April	0.98	0.136	0.84	0.65	1.59
May	0.97	0.135	0.84	0.64	1.57
June	0.95	0.133	0.82	0.63	1.55
Mean	0.92	0.022	0.95	0.83	0.98

Appendix 3.2: continued

iii) GLOBAL RADIATION:

a) Yearly means for each locations:

Location	Mean	SEM	Median	Min	Max
Calculated	55.80	1.719	58.22	49.30	60.43
1	4.7	0.53	4.5	3.3	7.2
3	4.5	1.00	3.6	1.7	7.9
4	3.6	0.40	3.3	2.1	5.0
5	7.5	1.19	7.7	3.6	12.4
6	6.6	1.02	6.4	2.7	10.9
7	4.9	1.35	2.7	1.9	9.9
8	11.2	1.77	10.8	6.6	19.6
Mean	6.2	0.97	4.9	3.6	11.2

b) Monthly means for locations:

Month	Mean	SEM	Median	Min	Max
December	6.0	0.9	6.4	3.3	9.9
January	6.2	0.9	6.9	3.2	8.9
February	6.2	0.8	6.9	3.1	8.4
March	6.0	1.5	4.6	2.2	12.4
April	5.0	1.5	3.3	1.9	11.5
May	6.9	1.7	6.4	1.9	14.6
June	6.8	2.3	5.7	1.7	19.6
Mean	6.2	0.2	6.2	5.0	6.9

Appendix 3.3: Mean daily day and night air temperature (°C) observed in the open (large clearing) and shade (understorey) of *J. procera* and *A. gracilior* forest stand at Arba-gugu during March/April 1991.

		Day		Night	
Location	Julian day	Open	Shade	Open	Shade
1	76	20.5	18.2	14.0	14.5
	77	20.9	18.5	14.4	14.8
	78	20.5	18.2	14.2	14.4
Gap edge	81	22.9	20.9	16.6	16.6
	82	21.6	20.4	16.6	16.7
	83	14.4	14.1	12.1	12.2
2	85	18.9	17.2	14.3	14.7
	86	17.9	15.9	13.2	13.6
	87	16.7	15.5	14.8	15.4
3	89	18.3	16.2	13.3	13.8
	90	19.0	17.5	13.9	14.6
	91	16.7	15.9	13.3	14.2
	92	18.4	17.0	13.6	14.2
4	93	18.8	17.6	14.2	14.4
	94	20.8	18.8	14.4	14.7
	95	20.9	18.6	14.4	14.6
5	101	18.8	16.6	12.8	13.0
	102	19.8	17.2	12.6	12.6
	103	16.3	14.9	13.0	13.1
6	105	18.5	16.5	14.0	14.4
	106	21.5	17.8	15.1	15.2
	107	21.5	17.9	15.2	15.4
7	109	19.7	17.5	13.4	13.5
	110	16.9	15.8	13.4	13.9
	111	18.5	16.8	13.4	13.5
	112	18.4	17.0	13.5	13.9

Appendix 4.1: Analysis of variance for *Juniperus procera* and *Afrocarpus gracilior* forest stand artificial (sown seeds) regeneration in response ground preparations under field conditions. Three-way ANOVA.

i) Analysis of variance for *J. procera* sown seed germinaton percent on arcsin transformation:

Source of Variation	Degrees of freedom (DF)	Sum of Squares (SS)	Mean of Squares (MS)	Variance Ratio *(F)*	Level of significance *(P)*
Row	2	0.705	0.352	0.019	0.981
Column	2	209.627	1.001	0.054	0.949
Ground preparation	2	336.376	168.188	9.080	0.099
Cultivation	1	74.589	74.589	40.31	0.000
Ground preparation * Cultivation interaction	2	37.047	18.523	10.01	0.007
Error	8	14.802	1.850		
Total	17	673.146			

ii) Analysis of variance for *A. gracilior* sown seed germination percent on arcsin transformation:

Source	DF	SS	MS	*F*	*P*
Row	2	0.416	0.208	0.058	0.945
Column	2	12.208	1.650	0.464	0.683
Ground preparation	2	62.817	31.409	8.828	0.102
Cultivation	1	12.988	12.988	5.49	0.047
Ground preparation * Cultivation interaction	2	7.116	3.558	1.50	0.279
Error	8	18.937	2.367		
Total	17	114.483			

Appendix 4.1 continued.

iii) Analysis of variance for *J. procera* seedlings height growth (cm):

Source	DF	SS	MS	*F*	*P*
Block	2	2.651	1.325	3.13	0.066
Plot	2	0.357	0.179	0.42	0.662
Ground preparation	2	576.709	288.355	680.97	0.000
Error	20	8.469	0.423		
Total	26	588.186			

iv) Analysis of variance for *A. gracilior* seedlings height growth (cm)

Source	DF	SS	MS	*F*	*P*
Block	2	1.0683	0.5342	2.05	0.155
Plot	2	0.7514	0.3757	1.44	0.260
Ground preparation	2	24.1753	12.0876	46.38	0.000
Error	20	5.2123	0.606		
Total	26	31.2073			

Appendix 4.2: Effect of ground preparation (burning and raking) and cultivation on the regeneration and growth of *J. procera* and *A. gracilior* following clear felling and timber extraction after 19 months. Duncan's multiple range test. Mean±(SE) preceded by the same letter(s) are not significantly different from each other at $P < 0.05$.

i) *J. procera* germination and survival (%):

Ground preparation	No cultivation	Cultivation	Mean
Control	d0.67±0.16	c4.67 ±0.57	2.67±0.63
Raking	b8.33±1.33	a11.78±0.70	b10.06±0.88
Burning	a12.78±1.34	a13.89±1.54	a13.33 ±1.06
Mean	b7.26±1.17	b10.11±0.98	8.69±0.78

ii) *A. gracilior* germination survival (%):

Ground preparation	No cultivation	Cultivation	Mean
Control	a4.44±1.83	ab3.78±0.68	a4.11±1.01
Raking	a5.44±0.85	a4.89±1.15	a5.17±0.74
Burning	ab3.11±0.74	b1.33±0.22	b2.22±0.45
Mean	a4.33±0.75	ab3.33±0.54	3.83±0.47

iii) Natural regeneration (count per 80 m^2):

Species	Control	Raking	Burning	*F*	*P*
J.procera	c3.7 (1.2)	b75.0 (17.8)	a118.7 (17.4)	70.00	0.001

iv) Height growth (cm):

Variables	Control	Raking	Burning	*F*	*P*
J. procera	b8.0 (0.68)	c5.7 (0.40)	a16.4 (1.01)	680.97	0.000
A. gracilior	a7.8 (0.73)	a8.2 (0.42)	b6.0 (0.84)	46.38	0.000

Appendix 5.1: Analysis of variance for *Juniperus procera* and *Afrocarpus gracilior* seed pre-germination and light treatments in a controlled environment. Three-way ANOVA.

i) Analysis of variance for the effect of pre-germination treatment on the germination of *J. procera* in a glasshouse experiment.

Source	DF	SS	MS	*F*	*P*
Position	4	48.52	12.13	0.21	0.929
Treatment	4	1608.32	402.08	6.97	0.002
Error	16	922.70	57.67		
Total	24	2579.55			

ii) Analysis of variance for the effect of light on the germination of *J. procera* in a glasshouse experiment.

Source	DF	SS	MS	*F*	*P*
Position	4	126.21	31.55	0.42	0.789
Treatment	3	166.64	55.55	0.74	0.546
Error	12	895.04	74.59		
Total	19	1187.9			

iii) Analysis of variance for the effect of pre-germination treatment on the germination of *A. gracilior* in a glasshouse experiment.

Source	DF	SS	MS	F	*P*
Position	4	122.59	30.65	1.64	0.228
Treatment	3	3222.64	1074.21	57.52	0.000
Error	12	224.09	18.67		
Total	19	3569.32			

iv) Analysis of variance for the effect of light on the germination of *A. gracilior* in a glasshouse experiment.

Source	DF	SS	MS	*F*	*P*
Position	4	521.04	130.26	2.86	0.071
Treatment	3	1208.98	402.99	8.84	0.002
Error	12	547.2	45.6		
Total	19	2277.22			

Appendix 6.1: Analysis of variance for the effect of PPF and nutrient supply on the growth of *J. procera* and *A. gracilior* seedlings grown under treatment for 20 weeks in a glasshouse.

a) *J. procera*:

i. Analysis of variance for biomass relative growth rate, R (g g^{-1} wk^{-1}):

Sources	DF	SS	MS	F	P
Position	9	0.000421	0.00005	0.45	0.901
Light	2	0.042483	0.02124	203.70	0.000
Nutrient	1	0.022396	0.02240	214.77	0.000
Light * Nutrient	2	0.005728	0.00286	27.46	0.000
Error	45	0.004692	0.00010		
Total	59	0.075719			

ii. Analysis of variance for relative stem extension growth rate, (cm cm^{-1} wk^{-1}):

Sources	DF	SS	MS	F	P
Position	9	0.0010291	0.0001143	0.98	0.472
Light	2	0.0001761	0.0000880	0.75	0.477
Nutrient	1	0.0045452	0.0045452	38.81	0.000
Light * Nutrient	2	0.0002139	0.0001070	0.91	0.409
Error	45	0.0052704	0.0001171		
Total	59	0.0112347			

iii) Analysis of variance for net assimilation rate, E (g m^{-2} wk^{-1}):

Sources	DF	SS	MS	F	P
Position	9	0.36931	0.04103	0.79	0.629
Light	2	9.94048	4.97024	95.37	0.000
Nutrient	1	0.01897	0.01897	0.36	0.549
Light * Nutrient	2	0.06281	0.03141	0.60	0.552
Error	45	2.34511	0.05211		
Total	59	12.73667			

Appendix 6.1: continued

iv. Analysis of variance for leaf area ratio, F ($m^2\ g^{-1}$):

Sources	DF	SS	MS	F	P
Position	9	0.00255	0.00028	0.63	0.765
Light	2	0.00250	0.00125	2.78	0.072
Nutrient	1	0.01896	0.01896	42.18	0.000
Light * Nutrient	2	0.00031	0.00016	0.35	0.708
Error	45	0.02023	0.00045		
Total	59	0.04455			

v. Analysis of variance for specific leaf area, S ($m^2\ g^{-1}$):

Sources	DF	SS	MS	F	P
Position	9	0.015716	0.001746	0.85	0.577
Light	2	0.006830	0.003415	1.66	0.202
Nutrient	1	0.033568	0.033568	16.31	0.000
Light * Nutrient	2	0.002441	0.001221	0.59	0.557
Error	45	0.092620	0.002058		
Total	59	0.151174			

vi. Analysis of variance for leaf weight ratio, w:

Sources	DF	SS	MS	F	P
Position	9	0.015528	0.001725	1.48	0.185
Light	2	0.005375	0.002688	2.30	0.111
Nutrient	1	0.068160	0.068160	58.44	0.000
Light * Nutrient	2	0.01032	0.005163	4.43	0.018
Error	45	0.052481	0.001166		
Total	59	0.151870			

vii. Analysis of variance for stem weight ratio, *s*:

Sources	DF	SS	MS	*F*	*P*
Position	9	0.0092432	0.00103	1.52	0.169
Light	2	0.0305729	0.01529	22.67	0.000
Nutrient	1	0.0319769	0.03138	46.09	0.000
Light * Nutrient	2	0.0021943	0.00110	1.63	0.208
Error	45	0.0303396	0.00067		
Total	59	0.1034269			

viii. Analysis of variance for specific stem length, *L* (cm g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	9	225890	25099	2.12	0.048
Light	2	2712952	1356476	114.47	0.000
Nutrient	1	227131	227131	19.17	0.000
Light * Nutrient	2	131256	65628	5.54	0.007
Error	45	533251	11850		
Total	59	1810481			

ix. Analysis of variance for stem weight ratio, *r*:

Sources	DF	SS	MS	*F*	*P*
Position	9	0.017707	0.001967	1.75	0.104
Light	2	0.061521	0.030761	27.43	0.000
Nutrient	1	0.191285	0.191285	170.59	0.000
Light * Nutrient	2	0.021398	0.101699	9.54	0.000
Error	45	0.050460	0.001121		
Total	59	0.342371			

Appendix 6.1: continued

x. Analysis of variance for number of branches:

Sources	DF	SS	MS	*F*	*P*
Position	9	66.400	7.378	1.67	0.124
Light	2	556.433	278.217	63.04	0.000
Nutrient	1	493.067	493.067	111.72	0.000
Light*Nutrient	2	173.233	86.617	19.63	0.000
Error	45	198.600	4.413		
Total	59	1487.733			

xi. Analysis of variance for root length (cm):

Sources	DF	SS	MS	*F*	*P*
Position	4	159.50	39.88	0.53	0.712
Light	2	87.41	43.71	0.59	0.566
Nutrient	1	59.08	59.08	0.79	0.384
Light*Nutrient	2	36.79	18.40	0.25	0.784
Error	20	1490.84	74.54		
Total	29	1833.63			

xii. Analysis of variance for root:stem length ratio:

Sources	DF	SS	MS	*F*	*P*
Position	4	0.1796	0.0449	0.15	0.962
Light	2	3.3377	1.6688	5.48	0.013
Nutrient	1	11.7660	11.7660	38.67	0.000
Light*Nutrient	2	2.2595	1.1298	3.71	0.043
Error	20	6.0855	0.3043		
Total	29	23.6283			

b) *A. gracilior*:

i) Analysis of variance for biomass relative growth rate, R (g g^{-1} wk^{-1}):

Sources	DF	SS	MS	F	P
Position	9	0.002132	0.00024	1.64	0.134
Light	2	0.009304	0.00465	32.11	0.000
Nutrient	1	0.011261	0.01126	77.73	0.000
Light * Nutrient	2	0.002441	0.00122	8.42	0.001
Error	45	0.006520	0.00014		
Total	59	0.031658			

ii) Analysis of variance for relative stem extension rate, (cm cm^{-1} wk^{-1}):

Sources	DF	SS	MS	F	P
Position	9	0.0015490	0.0001721	2.05	0.055
Light	2	0.0012331	0.0006154	7.34	0.002
Nutrient	1	0.0124214	0.0124214	148.09	0.000
Light * Nutrient	2	0.0019220	0.0009610	11.46	0.000
Error	45	0.0037746	0.0000839		
Total	59	0.0208977			

iii) Analysis of variance for net assimilation rate, E (g m^{-2} wk^{-1}):

Sources	DF	SS	MS	F	P
Position	9	0.4632	0.0515	0.36	0.948
Light	2	15.3045	7.6522	53.59	0.000
Nutrient	1	0.0595	0.0595	0.42	0.522
Light * Nutrient	2	0.0867	0.0434	0.30	0.740
Error	45	6.4252	0.1428		
Total	59	22.3391			

Appendix 6.1: continued.

iv. Analysis of variance for leaf area ratio, F ($m^2\ g^{-1}$):

Sources	DF	SS	MS	F	P
Position	9	0.00328	0.00036	0.95	0.497
Light	2	0.03144	0.01572	40.82	0.000
Nutrient	1	0.01083	0.01083	28.12	0.000
Light * Nutrient	2	0.00081	0.00040	1.05	0.359
Error	45	0.01733	0.00039		
Total	59	0.06367			

v) Analysis of variance for specific leaf area, S ($m^2\ g^{-1}$):

Sources	DF	SS	MS	F	P
Position	9	0.020182	0.002242	1.29	0.266
Light	2	0.135322	0.067661	39.07	0.000
Nutrient	1	0.000470	0.000470	0.27	0.605
Light * Nutrient	2	0.003904	0.001952	1.13	0.333
Error	45	0.077940	0.001732		
Total	59	0.237819			

vi) Analysis of variance for leaf weight ratio, w:

Sources	DF	SS	MS	F	P
Position	9	0.01562	0.00174	1.40	0.216
Light	2	0.00021	0.00011	0.08	0.919
Nutrient	1	0.23965	0.23965	193.42	0.000
Light * Nutrient	2	0.00770	0.00385	3.11	0.054
Error	45	0.05576	0.00124		
Total	59	0.31895			

Appendix 6.1: continued.

vii. Analysis of variance for stem weight ratio, *s*:

Sources	DF	SS	MS	*F*	*P*
Position	9	0.0150913	0.0016768	1.97	0.066
Light	2	0.0065798	0.0032899	3.86	0.028
Nutrient	1	0.0001193	0.0001193	0.14	0.710
Light * Nutrient	2	0.0000524	0.0000262	0.03	0.970
Error	45	0.0383100	0.0008513		
Total	59	0.0601529			

viii. Analysis of variance for specific stem length, *L* (cm g^{-1})

Sources	DF	SS	MS	*F*	(*P*)
Position	9	49321	5480	1.97	0.066
Light	2	157545	78772	28.27	0.000
Nutrient	1	34221	34221	12.28	0.001
Light * Nutrient	2	21804	10902	3.91	0.027
Error	45	125404	2787		
Total	59	388295			

ix. Analysis of variance for stem weight ratio, *r*:

Sources	DF	SS	MS	*F*	*P*
Position	9	0.01795	0.00200	1.27	0.281
Light	2	0.00632	0.00316	2.01	0.146
Nutrient	1	0.22546	0.22546	143.23	0.000
Light * Nutrient	2	0.00777	0.00389	2.47	0.096
Error	45	0.07084	0.00157		
Total	59	0.32834			

Appendix 6.1: continued.

x. Analysis of variance for number of leaves:

Sources	DF	SS	MS	*F*	*P*
Position	9	1913.7	212.6	0.94	0.499
Light	2	2134.2	1067.1	4.73	0.014
Nutrient	1	1904.1	1904.1	8.43	0.006
Light * Nutrient	2	9671.4	4835.7	21.42	0.000
Error	45	10161.3	225.8		
Total	59	25784.7			

xi. Analysis of variance for root lenght (cm):

Sources	DF	SS	MS	*F*	*P*
Position	9	49704	5523	1.71	0.114
Light	2	17733	8867	2.75	0.074
Nutrient	1	29704	29704	9.22	0.004
Light * Nutrient	2	44744	22372	6.95	0.002
Error	45	144936	3221		
Total	59	286821			

xii. Analysis of variance for Root:stem length ratio:

Sources	DF	SS	MS	*F*	*P*
Position	9	8.4066	0.9341	1.53	0.167
Light	2	5.9185	2.9592	4.85	0.012
Nutrient	1	13.5869	13.5869	22.26	0.000
Light * Nutrient	2	33.0213	16.5106	27.05	0.000
Error	45	27.4683	0.6104		
Total	59	88.4015			

Appendix 6.2: Growth characteristics of *Juniperus procera A. gracilior* seedlings grown under different PPFs and low and high nutrient levels for 20 weeks in a glasshouse. Mean (±SE) of 10 seedlings for individual treatment, 20 and 30 seedlings for all light and all nutrient treatments respectively. Duncan's multiple range test. Means preceded by the same letter(s) are not significantly different from each other at $p < 0.05$.

a) *J. procera*:

i) Relative biomass growth rate (g g^{-1} wk^{-1}):

ii) Net assimilation rate (g m^{-2} wk^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	f0.054 (0.002)	e0.069 (0.002)	c0.061 (0.002)	c0.705 (0.032)	c0.612 (0.023)	c0.658 (0.019)
3.5	d0.080 (0.003)	b0.120 (0.002)	b0.100 (0.002)	b1.212 (0.043)	b1.143 (0.071)	b1.177 (0.035)
9.0	c0.095 (0.005)	a0.157 (0.002)	a0.122 (0.004)	a1.627 (0.121)	a1.682 (0.121)	a1.655 (0.057)
All	b0.076 (0.004)	a0.115 (0.007)	0.096 (0.003)	a1.181 (0.083	a1.146 (0.088)	1.163 (0.062)

iii) Relative stem extension rate (cm cm^{-1} wk^{-1}):

iv) Leaf area ratio (m^2 g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	b0.053 (0.003)	a0.066 (0.002)	a0.060 (0.002)	ab0.079 (0.004)	a0.114 (0.006)	a0.096 (0.004)
3.5	b0.054 (0.003)	a0.071 (0.003)	a0.063 (0.003)	b0.067 (0.004)	a0.109 (0.007)	ab0.088 (0.005)
9.0	b0.048 (0.003)	a0.070 (0.003)	a0.059 (0.003)	b0.065 (0.010)	ab0.095 (0.005)	b0.080 (0.005)
All	b0.052 (0.002)	a0.069 (0.002)	0.060 (0.003)	b0.070 (0.004)	a0.106 (0.004)	0.088 (0.006)

Appendix 6.2: continued.

v) Specific leaf area ($m^2\ g^{-1}$):

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	bc0.166 (0.011)	a0.222 (0.012)	a0.194 (0.009)
3.5	c0.150 (0.010)	ab0.207 (0.012)	ab0.178 (0.008)
9.0	bc0.153 (0.022)	ab0.183 (0.010)	b0.168 (0.010)
All	b0.157 (0.009)	a0.204 (0.007)	0.180 (0.013)

vi) Leaf weight ratio:

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	b0.479 (0.014)	a0.514 (0.007)	a0.496 (0.007)
3.5	bc0.455 (0.013)	a0.523 (0.009)	b0.489 (0.009)
9.0	c0.424 (0.013)	a0.523 (0.006)	c0.474 (0.011)
All	b0.453 (0.009)	a0.520 (0.004)	0.486 (0.011)

vii) Stem weight ratio:

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	b0.228 (0.008)	a0.263 (0.007)	a0.245 (0.006)
3.5	bc0.204 (0.010)	ab0.244 (0.009)	b0.224 (0.007)
9.0	c0.160 (0.007)	b0.222 (0.006)	c0.191 (0.007)
All	b0.197 (0.007)	a0.243 (0.005)	0.220 (0.008)

viii) Root weight ratio:

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	c0.293 (0.012)	d0.224 (0.012)	c0.258 (0.009)
3.5	b0.341 (0.008)	d0.232 (0.013)	b0.287 (0.012)
9.0	a0.416 (0.013)	d0.255 (0.006)	a0.336 (0.016)
All	a0.350 (0.011)	b0.237 (0.007)	0.293 (0.011)

Appendix 6.2: continued.

ix) Specific stem length (cm g^{-1}):

x) Root length (cm):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	a794 (52)	a799 (36)	a796 (27)	a395 (51)	a432 (35)	a414 (43)
3.5	b514 (39)	c355 (14)	b435 (23)	a450 (19)	a448 (34)	a449 (27)
9.0	c378 (29)	d183 (8)	c291 (27)	a425 (18)	a475 (32)	a450 (26)
All	a569 (41)	b446 (50)	507 (34)	a423 (29)	a452 (34)	437 (32)

xiii) Number of branches:

xiv) Number of whorls:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	c1.2 (0.6)	bc2.6 (0.6)	c1.9 (0.4)	a24 (0.8)	a27 (0.5)	a25.3 (0.5)
3.5	bc2.9 (0.7)	a9.0 (0.5)	b5.9 (0.7)	a27 (1.2)	a32 (0.9)	a29.5 (0.8)
9.0	b4.5 (0.8)	a14.2 (0.8)	a9.4 (1.0)	a26 (0.6)	a35 (1.3)	a30.2 (1.0)
All	b2.9 (0.5)	a8.6 (1.0)	5.73 (0.7)	a25.4 (0.6)	a31.2 (0.8)	28.3 (0.8)

Appendix 6.2: continued.

b) *A. gracilior*:

i) Relative biomass growth rate (g g^{-1} wk^{-1}):

ii) Net assimilation rate (g m^{-2} wk^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	d0.093 (0.004)	c0.114 (0.005)	c0.079 (0.002)	c0.904 (0.035)	d0.815 (0.037)	c0.865 (0.035)
3.5	c0.119 (0.003)	b0.135 (0.004)	b0.107 (0.002)	b1.386 (0.092)	b1.247 (0.206)	b1.303 (0.068)
9.0	c0.109 (0.003)	a0.155 (0.004)	a0.126 (0.004)	a2.064 (0.135	a2.104 (0.206)	a2.086 (0.123)
All	b0.096 (0.003)	a0.112 (0.005)	0.104 (0.003)	a1.468 (0.109)	a1.368 (0.121)	1.418 (0.081)

iii) Relative stem extension rate (cm cm^{-1} wk^{-1}):

iv) Leaf area ratio (m^2 g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	d0.034 (0.002)	c0.051 (0.003)	b0.042 (0.003)	bc0.104 (0.006)	a0.142 (0.007)	a0.124 (0.007)
3.5	d0.035 (0.002)	b0.061 (0.003)	ab0.048 (0.003)	c0.091 (0.009)	b0.110 (0.007)	b0.105 (0.007)
9.0	d0.031 (0.004)	a0.075 (0.004)	a0.053 (0.006)	e0.055 (0.004)	cd0.080 (0.007)	c0.068 (0.005)
All	b0.034 (0.002)	a0.062 (0.003)	0.048 (0.002)	b0.086 (0.007)	a0.112 (0.006)	0.099 (0.005)

Appendix 6.2: continued.

v) Specific leaf area ($m^2\ g^{-1}$):

vi) Leaf weight ratio:

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	a0.240 (0.013)	a0.266 (0.015)	b0.251 (0.015)	b0.436 (0.012)	a0.535 (0.013)	a0.494 (0.013)
3.5	ab0.215 0.021	b0.201 (0.011)	c0.213 (0.013)	b0.425 (0.009)	a0.551 (0.016)	a0.488 (0.016)
9.0	c0.136 (0.009)	c0.141 (0.011)	d0.139 (0.007)	b0.406 (0.007)	a0.560 (0.016)	a0.483 (0.020)
All	a0.199 (0.015)	a0.204 (0.010)	0.201 (0.009)	b0.428 (0.007)	a0.549 (0.008)	0.488 (0.009)

vii) Stem weight ratio:

viii) Root weight ratio:

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	b0.234 (0.007)	b0.231 (0.013)	b0.232 (0.007)	b0.331 (0.012)	c0.237 (0.017)	b0.275 (0.013)
3.5	b0.214 0.013	b0.214 (0.005)	c0.214 (0.007)	ab0.360 (0.010)	c0.235 (0.015)	ab0.298 (0.016)
9.0	b0.210 (0.011)	b0.205 (0.005)	c0.208 (0.006)	a0.384 (0.009)	c0.234 (0.015)	a0.309 (0.019)
All	a0.219 (0.006)	a0.217 (0.006)	0.218 (0.004)	a0.352 (0.008)	b0.236 (0.008)	0.294 (0.009)

Appendix 6.2: continued.

ix) Specific stem length (cm g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	b186 (26)	a265 (21)	b225 15
3.5	c112 (18)	b182 (11)	c147 (7)
9.0	c104 (14)	c99 (13)	d101 (9)
All	b134 (13)	a182 (15)	158 (10)

x) Root length (cm):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	24.0 (1.3)	21.2 (1.4)	22.6 (10.4)
3.5	29.5 (1.5)	24.0 (2.1)	26.8 (14.9)
9.0	28.7 (1.1)	21.7 (1.3)	25.2 (12.1)
All	27.4 (8.9)	22.3 (10.1)	24.8 (7.5)

Appendix 6.3: Analysis of variance for the effect of PPF and nutrient supply on the leaf characteristics of *J. procera* and *A. gracilior* seedlings grown under treatment for 20 weeks in a glasshouse.

a) *Juniperus procera*:

i. Analysis of variance for leaf thickness (μm):

Sources	DF	SS	MS	*F*	*P*
Position	4	3312.3	828.1	1.92	0.147
Light	2	54543.2	27271.6	63.09	0.000
Nutrient	1	717.8	717.8	1.66	0.212
Light * Nutrient	2	159.5	79.8	0.18	0.833
Error	20	8645.1	432.3		
Total	29	67378.0			

ii. Analysis of variance for palisade thickness (μm):

Sources	DF	SS	MS	*F*	*P*
Position	4	1207.2	301.8	2.72	0.059
Light	2	22109.1	11054.8	99.62	0.000
Nutrient	1	79.8	79.8	0.72	0.407
Light * Nutrient	2	5.9	3	0.03	0.974
Error	20	2219.4	111.0		
Total	29	25621.3			

iii. Analysis of variance for spongy mesophyll thickness (μm):

Sources	DF	SS	MS	*F*	*P*
Position	4	1039.8	259.9	1.30	0.303
Light	2	5968.9	2984.4	14.95	0.000
Nutrient	1	221.5	221.4	1.11	0.305
Light * Nutrient	2	218.6	109.3	0.55	0.587
Error	20	3993.7	199.7		
Total	29	11442.5			

Appendix 6.3: continued.

iv. Analysis of variance for palisade:spongy ratio:

Sources	DF	SS	MS	*F*	*P*
Position	4	0.10215	0.02554	0.53	0.712
Light	2	0.73034	0.36517	7.64	0.003
Nutrient	1	0.00244	0.00244	0.05	0.823
Light * Nutrient	2	0.03452	0.01726	0.36	0.701
Error	20	0.95605	0.04780		
Total	29	1.82552			

v. Analysis of variance for stomatal density (mm^{-2})

Sources	DF	SS	MS	*F*	*P*
Position	4	413.47	103.37	1.73	0.183
Light	2	459.89	229.95	3.85	0.039
Nutrient	1	48.07	48.07	0.80	0.380
Light * Nutrient	2	82.93	41.47	0.69	0.511
Error	20	1194.60	59.73		
Total	29	2198.97			

b) *Afrocarpus gracilior*

i. Analysis of variance for leaf thickness (μm):

Sources	DF	SS	MS	*F*	*P*
Position	4	370.2	92.6	0.39	0.813
Light	2	28649.2	14324.6	60.37	0.000
Nutrient	1	98.5	98.5	0.41	0.527
Light * Nutrient	2	1047.7	523.8	2.21	0.136
Error	20	4746.0	237.3		
Total	29	34911.4			

Appendix 6.3: continued.

ii. Analysis of variance for palisade thickness (μm):

Sources	DF	SS	MS	*F*	*P*
Position	4	230.4	57.6	0.80	0.538
Light	2	8840.1	4420.1	61.58	0.000
Nutrient	1	35.4	35.4	0.49	0.490
Light * Nutrient	2	254.0	127.0	1.77	0.196
Error	20	1435.6	71.8		
Total	29	10795.6			

iii. Analysis of variance for spongy mesophyll thickness (μm):

Sources	DF	SS	MS	*F*	*P*
Position	4	275.70	68.92	0.80	0.542
Light	2	3463.97	1731.98	19.99	0.000
Nutrient	1	8.86	8.86	0.10	0.752
Light * Nutrient	2	431.27	215.64	2.49	0.108
Error	20	1732.97	86.65		
Total	29	5912.77			

iv. Analysis of variance for palisade:spongy ratio:

Sources	DF	SS	MS	*F*	*P*
Position	4	0.22227	0.05557	1.63	0.205
Light	2	0.23806	0.11903	3.50	0.050
Nutrient	1	0.00556	0.00556	0.16	0.690
Light * Nutrient	2	0.07799	0.03900	1.15	0.338
Error	20	0.68068	0.03403		
Total	29	1.22456			

Appendix 6.3: continued.

v. Analysis of variance for stomatal density (mm^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	4	2195.3	548.8	1.92	0.146
Light	2	10533.6	5266.8	18.47	0.000
Nutrient	1	1009.7	1009.7	3.54	0.075
Light * Nutrient	2	3119.0	1559.5	5.47	0.013
Error	20	5703.0	285.1		
Total	29	22560.9			

Appendix 6.4: Leaf characteristics of *J. procera* and *A. gracilior* seedlings grown under different PPFs and low and high nutrient levels for 20 weeks in a glasshouse. Mean of (±SE) 5, 10 and 15 seedlings for light, nutrient and individual treatments respectively. Duncan's multiple range test. Means followed by the same letter(s) are not significantly different from each other at $p < 0.05$.

a) *J. procera*:

Leaf thickness (μm):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	170c (6)	176c (11)	173c (6)
3.5	221b (5)	237b (12)	229b (7)
9.0	274a (7)	280a (15)	277a (8)
All	221a (12)	231a (13)	

Palisade thickness(μm):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	62c (3)	64c (4)	63c (3)
3.5	90b (9)	93b (3)	92b (4)
9.0	127a (5)	132a (6)	129a (4)
All	93a (8)	96a (8)	

Spongy thickness (μm):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	65bc (6)	67b (6)	66b (4)
3.5	85ab (2)	98a (8)	91a (4)
9.0	99a (3)	100a (10)	99a (5)
All	83a (4)	88a (6)	

Palisade:Spongy ratio:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	0.98b (0.09)	0.97b (0.06)	0.97b (0.05)
3.5	1.08ab (0.14)	0.97b (0.05)	1.02b (0.07)
9.0	1.30a (0.09)	1.36a (0.11)	1.33a (0.07)
All	1.12a (0.07)	1.10a (0.06)	

Appendix 6.4: continued.

Stomatal density (mm^{-2}):

Lower:upper leaf surface stomatal density ratio:

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	63b (4)	70ab (2)	67b (3)	2.04 (0.12)	1.88 (0.08)	1.96a (0.17)
3.5	67ab (4)	69ab (3)	68b (2)	1.85 (0.12)	1.99 (0.12)	1.92a (0.19)
9.0	76a (3)	75a (3)	76a (2)	1.65 (0.06)	1.78 (0.11)	1.72a (0.14)
All	69a (3)	71a (2)		1.85a (0.15)	1.88a (0.13)	

b) *A. gracilior*:

Leaf thickness (μm):

Palisade thickness(μm):

PPF ($mol\ m^{-2}\ d^{-1}$)	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	167c (3)	156cd (2)	162c (2)	68c (3)	67c (1)	68c (2)
3.5	191b (6)	178bc (8)	185b (5)	90b (2)	80b (5)	85b (3)
9.0	229a (7)	242a (10)	236a (6)	108a (3)	112a (6)	110a (3)
All	196a (7)	192a (11)		89a (5)	87a (6)	

Appendix 6.4: continued.

Spongy thickness (μm):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	76b (3)	66b (3)	71b (3)
3.5	76b (4)	74b (4)	75b (3)
9.0	91a (7)	100a (3)	96a (4)
All	81a (4)	80a (3)	

Palisade:Spongy ratio:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	0.91b (0.08)	1.03ab (0.07)	0.97b (0.05)
3.5	1.19a (0.05)	1.10ab (0.09)	1.15a (0.05)
9.0	1.22 (0.15)	1.12ab (0.04)	1.17a (0.08)
All	1.11a (0.07)	1.08a (0.06)	

Stomatal density (mm^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	122b (6)	126b (2)	124b (3)
3.5	128b (7)	130b (3)	129b (4)
9.0	186a (14)	146b (3)	166a (10)
All	146a (9)	134a (3)	

Lower/upper leaf surface stomatal density ratio:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	8.6 (0.4)	9.0 (0.21)	8.7a (1.3)
3.5	8.8 (0.6)	8.9 (0.2)	8.6a (0.6)
9.0	13.0 (1.0)	10.5 (0.2)	13.0a (1.5)
All	10.8a (0.9)	9.1a (0.8)	

Appendix 6.5: Analysis of variance for the effect of PPFs and nutrient supply on leaf dry weight, leaf chlorophylls and nitrogen contents of *J. procera* and *A. gracilior* seedlings grown under treatment for 20 weeks in a glasshouse.

a) *J. procera*:

i. Analysis of variance for leaf dry weight (g m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	4	253.3	63.3	2.2	0.111
Light	2	5806.7	2903.3	99.0	0.000
Nutrient	1	1333.3	1333.3	45.5	0.000
Light * Nutrient	2	206.7	103.3	3.5	0.049
Error	20	586.7	29.3		
Total	29	8186.7			

ii. Analysis of variance for chlorophylls *a*+*b* (mg m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	4	38592	9648	0.71	0.594
Light	2	637	319	0.02	0.977
Nutrient	1	447512	447512	32.96	0.000
Light * Nutrient	2	5109	2554	0.19	0.830
Error	20	271525	13576		
Total	29	763376			

iii. Analysis of variance for leaf chlorophyll *a* (mg m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	4	16977	4244	0.45	0.768
Light	2	1782	891	0.10	0.909
Nutrient	1	427909	427909	45.81	0.000
Light* Nutrient	2	9186	4593	0.49	0.619
Error	20	186833	9342		
Total	29	642688			

Appendix 6.5: continued.

iv. Analysis of variance for leaf chlorophyll *b* (mg m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	4	6449	1612	1.20	0.342
Light	2	609	304	0.23	0.800
Nutrient	1	218	218	0.16	0.692
Light * Nutrient	2	1227	614	0.46	0.640
Error	20	26918	1346		
Total	29	35422			

v. Analysis of variance for leaf chlorophyll *a*+*b* (mg g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	4	15.895	3.974	1.41	0.266
Light	2	94.722	47.361	16.85	0.000
Nutrient	1	212.231	212.231	75.52	0.000
Light * Nutrient	2	6.062	3.031	1.08	0.359
Error	20	56.204	2.810		
Total	29	385.114			

vi. Analysis of variance for leaf chlorophyll *a* (mg g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	4	10.238	2.560	1.15	0.363
Light	2	57.528	28.764	12.90	0.000
Nutrient	1	177.137	177.137	79.43	0.000
Light * Nutrient	2	5.090	2.545	1.14	0.338
Error	20	44.601	2.230		
Total	29	294.595			

Appendix 6.5: continued.

vii. Analysis of variance for leaf chlorophyll *b* (mg g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	4	1.3959	0.3490	1.63	0.205
Light	2	4.9174	2.4587	11.50	0.000
Nutrient	1	1.5985	1.5985	7.48	0.013
Light * Nutrient	2	0.2891	0.1445	0.68	0.520
Error	20	4.2770	0.2138		
Total	29	12.4778			

viii. Analysis of variance for leaf chlorophyll *a:b* ratio:

Sources	DF	SS	MS	*F*	*P*
Position	4	3.0194	0.7549	0.81	0.534
Light	2	1.8147	0.9074	0.97	0.395
Nutrient	1	20.6200	20.6200	22.11	0.000
Light * Nutrient	2	2.1781	1.0891	1.17	0.331
Error	20	18.6549	0.9327		
Total	29	46.2871			

ix. Analysis of variance for leaf nitrogen content (%):

Sources	DF	SS	MS	*F*	*P*
Position	4	2.8055	0.3117	0.94	0.497
Light	2	0.5017	0.2508	0.76	0.474
Nutrient	1	21.8286	21.8286	66.13	0.000
Light*Nutrient	2	0.2208	0.1104	0.33	0.717
Error	20	14.8535	0.3301		
Total	29	40.2100			

Appendix 6.5: continued.

b) *A. gracilior*:

i. Analysis of variance for leaf dry weight (g m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	6	793.7	132.3	0.78	0.596
Light	2	10176.1	5088.1	29.81	0.000
Nutrient	1	257.5	257.5	1.51	0.229
Light*Nutrient	2	178.9	89.5	0.52	0.597
Error	30	5119.8	170.7		
Total	41	16526.0			

ii. Analysis of variance for chlorophylls *a*+*b* (mg m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	6	63293	10549	1.00	0.444
Light	2	84368	42184	4.00	0.029
Nutrient	1	770182	770182	72.96	0.000
Light*Nutrient	2	54322	27161	2.57	0.093
Error	30	316682	10556		
Total	41	1288847			

iii. Analysis of variance for leaf chlorophyll *a* (mg m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	6	52809	8802	1.14	0.364
Light	2	56462	28231	3.65	0.038
Nutrient	1	418441	418441	54.15	0.000
Light*Nutrient	2	48810	24405	3.16	0.057
Error	30	231821	7727		
Total	41	808343			

Appendix 6.5: continued.

iv. Analysis of variance for leaf chlorophyll *b* (mg m^{-2}):

Sources	DF	SS	MS	*F*	*P*
Position	6	12186.2	2031.0	2.32	0.059
Light	2	3163.0	1581.5	1.80	0.182
Nutrient	1	53196.4	53196.4	60.64	0.000
Light*Nutrient	2	146.5	73.3	0.08	0.920
Error	30	26318.7	877.3		
Total	41	95010.8			

v. Analysis of variance for leaf chlorophyll *a*+*b* (mg g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	6	19.301	3.217	1.51	0.209
Light	2	458.914	229.457	107.61	0.000
Nutrient	1	338.596	338.596	158.80	0.000
Light*Nutrient	2	13.925	6.962	3.27	0.052
Error	30	63.968	2.132		
Total	41	894.704			

vi. Analysis of variance for leaf chlorophyll *a* (mg g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	6	13.127	2.188	1.56	0.194
Light	2	251.503	125.751	89.51	0.000
Nutrient	1	174.689	174.689	124.34	0.000
Light*Nutrient	2	11.641	5.820	4.14	0.026
Error	30	42.148	1.405		
Total	41	493.108			

Appendix 6.5: continued.

vii. Analysis of variance for leaf chlorophyll *b* (mg g^{-1}):

Sources	DF	SS	MS	*F*	*P*
Position	6	6.0596	1.0099	2.33	0.058
Light	2	31.1627	15.5814	35.92	0.000
Nutrient	1	26.8896	26.8896	62.98	0.000
Light*Nutrient	2	0.4187	0.2093	0.48	0.622
Error	30	13.0151	0.4338		
Total	41	77.5458			

viii. Analysis of variance for leaf chlorophyll *a/b* ratio:

Sources	DF	SS	MS	*F*	*P*
Position	6	7.0474	1.1746	1.88	0.117
Light	2	1.1736	0.5868	0.94	0.408
Nutrient	1	0.6684	0.6684	1.07	0.313
Light*Nutrient	2	4.0092	2.0046	3.21	0.055
Error	30	18.7542	0.6251		
Total	41	31.6527			

ix. Analysis of variance for leaf nitrogen content (%):

Sources	DF	SS	MS	*F*	*P*
Position	9	2.0136	0.2237	1.59	0.147
Light	2	2.7572	1.3786	9.81	0.000
Nutrient	1	22.5829	22.5829	169.72	0.000
Light*Nutrient	2	0.1881	0.0941	0.67	0.517
Error	45	6.3229	0.1405		
Total	59	33.8648			

Appendix 6.6: Effect of light and nutrient supply on leaf dry weight, leaf chlorophylls and leaf nitrogen content of *J. procera* and *A. gracilior* seedlings grown in a glasshouse under different PPFs and high and low nutrient treatments for 20 weeks. Duncan's multiple range test. Mean (±SE) 15, 10 and 5 seedlings for light, nutrient and individual treatments respectively. Means followed by the same letter(s) are not significantly different from each other at $P < 0.05$.

a) *J. procera*:

Chlorophyll *a+b* (mg g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	8.7b (0.4)	14.0a (0.9)	11.3a (1.0)
3.5	5.9c (0.8)	12.4a (0.9)	9.1b (1.2)
9.0	4.9c (0.6	9.1b (0.9)	7.0c (0.9)
All	6.5b (0.5)	11.8a (0.7)	

Chlorophyll *a* (mg g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	6.6b (0.5)	11.3a (1.0)	8.9a (0.9)
3.5	4.4c (0.4)	10.4a (0.8)	7.4b (1.1)
9.0	3.6c (0.4)	7.5b (0.7)	5.5c (0.8)
All	4.9b (0.4)	9.7a (0.6)	

Chlorophyll *b* (mg g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	2.1ab (0.1)	2.8a (0.2)	2.4a (0.2)
3.5	1.5b (0.3)	1.9b (0.2)	1.7b (0.2)
9.0	1.3b (0.1)	1.5b (0.1)	1.4b (0.1)
All	1.6b (0.2)	2.1a (0.2)	

Chlorophyll *a+b* (mg m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	483b (28)	701a (47)	592a (44)
3.5	455b (68)	735a (43)	595a (60)
9.0	466b (57)	702a (53)	584a (54)
All	468b (29)	713a (26)	

Appendix 6.6: continued.

Chlorophyll *a* (mg m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	369b (26)	563a (51)	466a (42)
3.5	339b (41)	620a (41)	479a (54)
9.0	340b (34)	582a (48)	461a (49)
All	350b (19)	588a (26)	

Chlorophyll *b* (mg m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	115a (9)	138a (9)	126a (7)
3.5	116a (29)	115a (7)	116a (14)
9.0	126a (24)	119a (7)	123a (12)
All	119a (12)	124a (5)	

Chlorophyll *a:b* Ratio:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	3.27b (0.32)	4.19ab (0.55)	3.73a (0.34)
3.5	3.23b (0.35)	5.43a (0.45)	4.33a (0.45)
9.0	3.02b (0.48)	4.88a (0.48)	3.95a (0.42)
All	3.18b (0.21)	4.83a (0.28)	

Leaf dry weight (g m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	56c (2)	50c (1)	53c (1)
3.5	76b (2)	60c (3)	68b (3)
9.0	96a (2)	78b (3)	87a (3)
All	76a (4)	63b (3)	

Appendix 6.6: continued.

Leaf Nitrogen percent:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	0.85b (0.11)	2.20a (0.25)	1.52a (0.19)
3.5	1.00b (0.08)	2.18a (0.21)	1.59a (0.18)
9.0	0.83b (0.05)	2.18a (0.21)	1.51a (0.18)
All	0.89b (0.05)	2.19a (0.14)	

b) *A. gracilior*:

Chlorophyll *a+b* (mg g^{-1}):

Chlorophyll *a* (mg g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	11.8b (0.8)	16.2a (0.5)	14.0a (0.7)	8.7b (0.7)	11.5a (0.4)	10.1a (0.6)
3.5	5.9d (0.8)	13.1b (0.2)	9.5b (1.1)	4.3d (0.7)	9.6b (0.3)	6.9b (0.8)
9.0	3.1e (0.2)	8.6c (0.7)	5.9c (0.8)	2.1e (0.1)	6.2c (0.3)	4.1c (0.6)
All	6.9b (0.9)	12.6a (0.7)		4.0b (0.7)	9.1a (0.5)	

Appendix 6.6: continued.

Chlorophyll *b* (mg g^{-1}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	3.1b (0.3)	4.7a (0.3)	3.9a (0.3)
3.5	1.7d (0.1)	3.5b (0.2)	2.6b (0.3)
9.0	1.1d (0.1)	2.5c (0.4)	1.8c (0.3)
All	2.0b	3.6a	

Chlorophyll *a+b* (mg m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	444b (40)	619a (41)	531a (37)
3.5	327c (40)	616a (37)	471ab (48)
9.0	248c (20)	596a (49)	422b (55)
All	339b	610a	

Chlorophyll a (mg m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	332b (40)	441a (35)	386a (30)
3.5	234c (34)	451a (30)	342ab (37)
9.0	160c (14)	433a (41)	296b (43)
All	242b (23)	441a (20)	

Chlorophyll *b* (mg m^{-2}):

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	112b (9)	178a (13)	145a (12)
3.5	92b (6)	165a (12)	129ab (12)
9.0	88b (11)	163a (20)	126b (15)
All	98b (5)	169a (8)	

Appendix 6.6: continued.

Chlorophyll a:b Ratio:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	3.07a (0.50)	2.53ab (0.24)	2.80a (0.28)
3.5	2.46ab (0.20)	2.80ab (0.24)	2.63a (0.16)
9.0	1.91b (0.18)	2.88ab (0.42)	2.39a (0.26)
All	2.48a (0.21)	2.74a (0.18)	

Leaf dry weight (g m^{-2}):

	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	38c (2)	38c (2)	38c (1)
3.5	56b (3)	47.bc (2)	52b (2)
9.0	79a (5.03)	72a (9)	76a (5)
All	57a (4)	53a (5)	

Leaf Nitrogen percent:

PPF (mol m^{-2} d^{-1})	Nutrient mg l^{-1} nitrogen 1	30	All
2.0	1.33b (0.20)	2.44a (0.18)	1.89a (0.20)
3.5	0.95c (0.07)	2.15a (0.13)	1.55ab (0.18)
9.0	0.68d (0.06)	2.06a (0.18)	1.37b (0.21)
All	0.99b (0.08)	2.22a (0.08)	